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COMPORTEMENT DYNAMIQUE DES PRÉDATEURS ET DES PROIES DANS UN SYSTÈME À PLUSIEURS HABITATS

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ANGÉLIQUE DUPUCH

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RÉSUMÉ

Comprendre les interactions prédateurs-proies et notamment la réponse de l'un vis-à-vis de l'autre est un sujet central en écologie. Beaucoup d'études se sont penchées sur l'utilisation des habitats par les prédateurs et les proies, et ont montré que les proies préféraient les habitats pauvres en prédateurs et inversement, que les prédateurs préféraient les habitats riches en proies. Cependant, la plupart de ces études ont exploré le comportement des prédateurs et des proies en fixant l'un ou l'autre dans l'espace. Les connaissances théoriques et empiriques sur l'utilisation des habitats par les prédateurs et les proies quand les deux peuvent se déplacer librement sont peu abondantes. Cette thèse s'inscrit dans ce contexte et s'intéresse au comportement anti-prédateur et à la sélection de l'habitat par une espèce-proie, le ventre rouge du nord (*Phoxinus eos*), lorsqu'elle est confrontée à un risque de prédation qui varie en intensité, dans le temps et dans l'espace. Dans une première expérience, l'étude de l'intensité de la réponse des ventres rouges du nord soumis à différentes concentrations de substance chimique d'alerte a permis de vérifier que cette espèce était capable de détecter différents degrés dans le risque de prédation et d'y adapter l'intensité de sa réponse anti-prédateur. Des expériences d'attachement effectuées en lacs ont ensuite montré que le risque relatif de prédation du ventre rouge du nord était plus élevé (i) le jour que la nuit et (ii) dans la zone pélagique profonde que dans les zones pélagique supérieure et littorale. L'utilisation des zones littorale et pélagique par les ventres rouges du nord coïncide avec les variations spatiales et temporelles de leur risque de prédation, et supporte l'hypothèse que les migrations nycthémérales entre les zones littorale et pélagique des lacs leur permettent de réduire leur risque de prédation, tout en maximisant leur taux d'alimentation sur le zooplancton. De plus, la corrélation positive entre l'abondance des ventres rouges du nord dans la zone littorale des lacs étudiés et le risque relatif de prédation dans la zone pélagique supporte l'hypothèse que cette espèce utilise la zone littorale pour réduire son risque de prédation par les prédateurs pélagiques. Le fait que l'omble de fontaine (*Salvelinus fontinalis*; principal prédateur du ventre rouge du nord dans ce système) soit rarement observé dans la zone littorale et la présence d'habitats structurés dans cette dernière expliqueraient en partie la préférence du ventre rouge du nord pour la zone littorale durant la journée. A l'échelle de la zone littorale, l'étude de l'abondance des ventres rouges du nord dans les habitats structurés et sans structure (i) a montré que cette espèce utilisait préférentiellement les habitats structurés et (ii) suggère que cette espèce ne répond pas à l'augmentation du risque de prédation par une utilisation accrue des habitats structurés, contrairement à ce qui est généralement observé chez les poissons. Cette divergence s'expliquerait par la flexibilité de ses stratégies anti-prédateurs. La préférence des ventres rouges du nord pour les habitats pauvres en prédateurs et riches en structures a été confirmée par des expériences effectuées en laboratoire. Ces expériences ont également montré qu'en absence de prédateurs, la distribution spatiale des ventres rouges du nord était

positivement et essentiellement reliée à la distribution spatiale de la ressource alimentaire. Cependant, les résultats d'expériences avec des prédateurs libres de se déplacer indiquent (i) que l'influence de la distribution de la ressource et du risque inhérent à l'habitat (p. ex., la complexité structurelle de l'habitat) sur la distribution des ventres rouges du nord diminue et augmente respectivement avec l'intensité du risque de prédation, et (ii) que l'évitement des prédateurs détermine le choix de l'habitat par les ventres rouges du nord quand le risque de prédation est élevé. Ces résultats sont cohérents avec le comportement du ventre rouge du nord en lac. Ce projet de doctorat a montré que, dans les systèmes où le risque de prédation varie en intensité dans le temps et dans l'espace, les réponses et les tactiques anti-prédateurs des proies sont flexibles et fortement influencées par l'intensité du risque de prédation. Il en résulte une sélection dynamique de l'habitat par les proies, qui peut se traduire dans les milieux naturels, par une forte variabilité spatiale et temporelle de leurs patrons de distribution.

Mots clés : écologie comportementale, distribution idéale et libre, interactions prédateurs-proies, risque de prédation, sélection de l'habitat.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

CHAPITRE II

CHAPITRE III

CHAPITRE IV

LISTE DES FIGURES

CHAPITRE I

CHAPITRE II

CHAPITRE III

CHAPITRE IV

INTRODUCTION GÉNÉRALE

Les interactions prédateur-proie ont depuis longtemps attiré l'attention des écologistes. La principale raison est que la prédation entraîne inévitablement la mort d'individus (Taylor 1984), ce qui peut avoir des conséquences importantes sur la dynamique des populations et sur les écosystèmes. En plus de l'effet létal de la prédation, la présence de prédateurs peut aussi entraîner des changements dans le comportement des proies qui tentent de réduire leur risque d'être la victime d'un prédateur (Lima et Dill 1990; Lima 1998a, 1998b). Ainsi, les prédateurs peuvent avoir un impact important sur les systèmes écologiques indépendamment de l'effet létal de la prédation, dû à la flexibilité du comportement des proies (Lima 1998a). Un aspect comportemental important dans les interactions prédateur-proie est celui de la sélection de l'habitat par les prédateurs et les proies. En effet, les décisions liées à l'utilisation des habitats par les prédateurs et les proies déterminent le degré de chevauchement spatial entre les deux, ce qui affecte leur taux de rencontre, les taux de prédation et finalement, la dynamique des populations et des communautés prédateur-proie (Schmitz 2005).

En général, l'utilisation des habitats par les organismes intègre des décisions comportementales qui influencent les différentes composantes de la valeur adaptative (angl.: fitness) des individus, telles que le taux d'alimentation, le taux de survie et le taux de reproduction (Sutherland 1996). Les organismes mobiles tels que les poissons ou les oiseaux sélectionnent les habitats principalement en fonction de leurs caractéristiques physiques, de la densité des ressources, du risque de prédation et de la présence de congénères (Cody 1985; Kramer *et al.* 1997). En dehors de la période de reproduction, les organismes préfèrent généralement les habitats leur permettant d'avoir un taux d'alimentation élevé, le plus souvent des habitats offrant la plus grande quantité de ressources alimentaires (Stephen et Krebs 1986) et un risque de prédation faible (Lima et Dill 1990; Lima 1998b). Cependant, les habitats offrant le plus de nourriture sont généralement aussi les plus risqués, ce qui oblige les

organismes à adopter un comportement leur permettant de maximiser leur alimentation tout en minimisant le risque de mortalité dû à la prédation (Lima et Dill 1990). On peut donc s'attendre à ce que la sélection naturelle favorise les individus capables d'estimer les coûts et les bénéfices liés à l'utilisation d'un habitat. Par exemple, l'utilisation d'un refuge est souvent associée à une perte de temps consacré à l'alimentation (Sih 1997). Plus un individu reste caché dans un refuge, plus ses chances d'être là victime d'un prédateur diminuent, mais plus les coûts énergétiques (dus aux opportunités de s'alimenter perdues) augmentent. Par conséquent, les individus doivent être capables de reconnaître le niveau de risque que représente un prédateur donné et d'adapter leur comportement en fonction de l'intensité du risque de prédation (Helfman 1989; Zhao et Chivers 2005).

Beaucoup de systèmes naturels sont constitués de prédateurs et de proies qui peuvent se déplacer librement entre des habitats qui diffèrent dans leurs caractéristiques biotiques et abiotiques. Par conséquent, les patrons spatiaux et temporels de la ressource alimentaire et du risque de prédation des proies ne sont pas uniformes (p. ex., Post *et al.* 1998; Danilowicz et Sale 1999; Creel et Winnie 2005). Les proies doivent donc adapter leur utilisation des habitats dans le temps et dans l'espace. Les déplacements réguliers entre des sites d'alimentation et des refuges comme par exemple chez les poissons des récifs coralliens et d'eau douce (Helfman 1993; Reebs 2002), le krill (Alonzo *et al.* 2002), le zooplancton d'une manière générale (De Meester *et al.* 1999) et le babouin (*Papio cynocephalus ursinus*; Cowlishaw 1997) en sont de bons exemples. L'hétérogénéité du risque de prédation provient de la variation des facteurs associés aux habitats (p. ex., le degré de complexité structurelle, la luminosité) et aux prédateurs (p. ex., leur densité, leur distribution spatiale). On peut donc s'attendre à ce que les proies prennent en compte ces deux types de facteurs au moment de choisir un habitat. Beaucoup d'études ont montré qu'à échelle locale, les proies augmentent l'utilisation des habitats à structure complexe (tels que les zones avec végétation) quand le risque de prédation est élevé (Lima et Dill 1990; Lima 1998b) et qu'à plus grande échelle, elles évitent les habitats

pauvres en refuges ou riches en prédateurs (p. ex., la zone pélagique des lacs; Lima 1998b). D'un autre côté, étant donné que les opportunités de s'alimenter pour les prédateurs dépendent fortement du patron de distribution de leurs proies, on peut s'attendre à ce que les prédateurs suivent de près leurs proies. Ainsi, les prédateurs et les proies sont pris dans un "jeu", à l'intérieur duquel la distribution spatiale de l'un influence la distribution spatiale de l'autre (Sih 2005). Un grand nombre d'études ont exploré l'utilisation des habitats par les prédateurs et les proies (Lima et Dill 1990; Lima 1998b), mais la plupart se sont intéressées au comportement de l'un en fixant la distribution de l'autre dans l'espace (p. ex., en mettant le prédateur en cage).

Lima (2002) a souligné le manque de connaissances théoriques et empiriques sur les conséquences de l'utilisation des habitats par les prédateurs et les proies quand les deux peuvent se déplacer librement. Ce sujet a été traité dans plusieurs études théoriques qui ont utilisé la théorie des jeux (Maynard Smith 1982) comme cadre conceptuel de leur modèle (p. ex., Hugie et Dill 1994; Sih 1998; Bouskila 2001; Alonzo 2002; Krivan et Schmit 2003; Luttbeg et Sih 2004). En général, ces études ont utilisé le modèle de la Distribution Idéale et Libre (Fretwell et Lucas 1970; Kacelnik *et al.* 1992) pour examiner des systèmes à trois niveaux trophiques (ressource, proie, prédateur), dans lesquels les prédateurs et les proies sont libres de se déplacer entre des habitats qui diffèrent en terme de profitabilité et/ou de risque inhérent à l'habitat (i.e., une mesure du risque de prédation qui est indépendante de la densité de prédateurs, telle que le niveau de complexité structurel dans l'habitat; Hugie et Dill 1994). Une prédiction commune à ces modèles est que la distribution des proies ne devrait pas (ou presque pas) être influencée par la distribution de la ressource alimentaire. De plus, si le risque inhérent à l'habitat varie, les modèles prédisent que la distribution des proies devrait être principalement influencée par le risque inhérent à l'habitat, les proies évitant les habitats les plus risqués, quelle que soit la distribution de la ressource alimentaire (Hugie et Dill 1994; Sih 1998; Luttbeg et Sih 2004). Cette prédiction est assez différente des résultats provenant d'études théoriques et empiriques qui incorporent une différence "fixe" du risque de prédation

entre les habitats (i.e., un habitat est toujours considéré comme plus risqué que l'autre). En effet, dans un tel contexte, plusieurs études ont montré que les proies considéraient à la fois la distribution de la ressource et le risque de prédation quand elles choisissaient un habitat où s'alimenter (Gilliam et Fraser 1987; Abrahams et Dill 1989; Lima et Dill 1990; Grand et Dill 1997).

Très peu d'études empiriques se sont intéressées à la sélection de l'habitat par les prédateurs et les proies lorsque les deux sont mobiles (Sih 1984; Formanowicz et Bobka 1989; Bouskila 2001; Sih 2005; Hammond *et al.* 2007). Mon projet de doctorat s'inscrit dans un tel contexte et s'intéresse plus particulièrement au choix de l'habitat par la proie lorsqu'elle est confrontée à un risque de prédation qui varie dans le temps et l'espace. Nous devions pour cela disposer d'un modèle où le comportement de la proie d'une part, et le risque de prédation d'autre part soient variables et facilement identifiables.

Le ventre rouge du nord (*Phoxinus eos*) effectue des migrations nycthémérales du large au rivage dans des petits lacs oligotrophes du bouclier canadien (Naud et Magnan 1988; Gauthier *et al.* 1997). Les individus nagent en banc dans la zone littorale le jour, migrent dans la zone pélagique (où les bancs se dispersent) au coucher du soleil, pour s'alimenter sur le zooplancton, et retournent ensuite en zone littorale au lever du soleil. Il existe une certaine variabilité autour de ce patron général, un petit nombre d'individus étant observé en dehors de la zone littorale durant le jour (Naud et Magnan, 1988; Comeau et Boisclair 1998; Gaudreau et Boisclair 1998). Naud et Magnan (1988) ont suggéré que le ventre rouge du nord utilisait la zone littorale durant le jour pour réduire le risque de prédation par l'omble de fontaine, *Salvelinus fontinalis,* un prédateur visuel (Power 1980). En accord avec cette hypothèse, Gaudreau et Boisclair (1998) ont montré que la présence de prédateurs pélagiques tels que l'omble de fontaine réduisait significativement le nombre de ventre rouge du nord présent dans la zone pélagique, en particulier durant la nuit. De plus, le ventre rouge du nord montre une préférence pour les habitats à structure complexe tels que les zones avec végétation et les structures ligneuses

submergées (p. ex., les branches d'un arbre mort) dans la zone littorale des lacs (Naud et Magnan 1988; He et Lodge 1990; MacRae et Jackson 2001; Jacobus et Ivan 2005). Beaucoup d'études ont montré que la densité des poissons était plus élevée dans les zones avec végétation (p. ex., Lewin et al. 2004) et plusieurs d'entre elles suggèrent que les individus utilisent ces habitats pour réduire leur risque de prédation. En laboratoire, l'utilisation des habitats structurés a permis au ventre rouge du nord de réduire significativement le nombre d'attaques et de captures par l'omble de fontaine (East et Magnan 1991), ce qui supporte l'hypothèse que les ventres rouges du nord utilisent ces habitats pour réduire leur risque de prédation.

Par ailleurs, des études antérieures ont montré que l'omble de fontaine se nourrissait de ventre rouge du nord (p. ex., East et Magnan 1991; Lacasse et Magnan 1992). De plus, l'occurrence de ventre rouge du nord dans l'alimentation de l'omble de fontaine était plus élevée dans les lacs contenant du meunier noir, *Catostomus commersonii*, et/ou du mulet à cornes, *Semotilus atromaculatus*, que dans les lacs contenant seulement de l'omble de fontaine (East et Magnan 1991; Tremblay et Magnan 1991; Lacasse et Magnan 1992). Ceci s'expliquerait par le fait que l'omble de fontaine déplace sa niche alimentaire des organismes benthiques vers les organismes pélagiques (tel que le ventre rouge du nord) en présence du meunier et du mulet, ces deux espèces étant mieux adaptées pour s'alimenter sur les proies benthiques que l'omble de fontaine (Magnan et Fitzgerald 1982; Magnan et Fitzgerald 1984; Tremblay et Magnan 1991; Bourke *et al.* 1999). Cela suggère que le risque de prédation sur le ventre rouge du nord est plus élevé dans les lacs contenant du meunier et/ou du mulet que dans les lacs contenant seulement de l'omble de fontaine (appelés ci-après lacs "avec compétiteurs" et "sans compétiteurs" respectivement). Ce système naturel est donc un bon modèle pour étudier en milieu naturel et en laboratoire (i) si les variations dans l'utilisation des habitats par les proies sont reliées aux variations spatio-temporelles du risque de prédation et (ii) quelles caractéristiques de l'habitat (telles que la quantité de ressources alimentaires et le degré de complexité structurelle) vont être prises en compte par la proie lors de

la sélection de l'habitat, lorsque les prédateurs et les proies sont tous les deux mobiles.

Dans un premier temps, nous avons vérifié en laboratoire si le ventre rouge du nord était capable de percevoir différents niveaux de risque de prédation et d'y adapter l'intensité de sa réponse anti-prédateur (Chapitre I). Pour répondre à cet objectif, nous avons utilisé la capacité qu'ont certaines espèces de cyprinidés et autres ostariophysiens (dont fait partie le ventre rouge du nord) à détecter un risque de prédation en se basant sur une substance chimique d'alerte (*sensu* Smith 1992). Cette substance est un composé chimique présent dans l'épiderme des individus et qui se répand dans l'eau après dommage mécanique de la peau (e.g. suite à une morsure par un prédateur). La substance chimique d'alerte obtenue à partir d'extrait de peau de ventre rouge du nord a été diluée à différentes concentrations (ce qui avait pour but de simuler différentes intensités de risque de prédation) et introduite dans l'eau d'un aquarium contenant 10 ventres rouges du nord. La distribution des individus dans l'aquarium, leur cohésion et leur orientation (i.e., le comportement de banc), les départs brusques (angl.: dashing) et les immobilisations prolongées (angl.: freezing) ont été estimés avant et après l'injection de la substance dans l'eau afin de caractériser la réaction de peur du ventre rouge du nord à différentes intensités de risque de prédation.

Les expériences en laboratoire et en milieu semi-naturels (p. ex., en enclos) ont fortement contribué à l'acquisition des connaissances sur la sélection de l'habitat par les proies, mais les expériences en milieu naturel ont été plus rares. Malgré leur manque de réalisme écologique, les expériences en laboratoire sont préférées aux expériences en milieu naturel parce qu'elles offrent l'avantage de pouvoir contrôler et mesurer le risque de prédation, chose quasi-impossible en milieu naturel. Cette difficulté fait que l'étude de Naud et Magnan (1988), comme beaucoup d'autres qui se sont intéressées à la distribution spatiale de proies dans leur milieu naturel, ne peut que suggérer le risque de prédation comme facteur expliquant les variations de la distribution spatiale du ventre rouge du nord. Nous avons donc fait des expériences

d'attachement (angl.: tethering experiments) afin d'estimer les patrons spatiaux et temporels du risque de prédation sur le ventre rouge du nord en lac (Chapitre II). Les objectifs spécifiques de cette expérience étaient de (i) déterminer si les migrations nycthémérales observées chez le ventre rouge du nord étaient reliées aux variations spatio-temporelles du risque de prédation (comme suggéré par Naud et Magnan 1988) et (ii) déterminer les facteurs influençant le risque de prédation sur le ventre rouge du nord. Des ventres rouges du nord ont été positionnés à différentes combinaisons d'isobathes et de profondeurs dans la colonne d'eau pour une période de 17 heures, dans 11 lacs du bouclier canadien (6 lacs sans compétiteurs, 5 lacs avec compétiteurs). Les individus étaient attachés à un système chronométrique permettant de déterminer l'heure à laquelle la prédation était survenue. Les patrons spatiaux et temporels du risque de prédation ont été déterminés à partir du nombre d'individus manquant après un temps donné d'exposition aux prédateurs. Les facteurs influençant le risque de prédation du ventre rouge du nord ont été déterminés à l'aide d'analyses de survie.

Nous avons également estimé l'abondance des ventres rouges du nord dans la zone littorale des lacs, dans deux types d'habitats : le premier contenant de la végétation ou des débris ligneux (appelés "habitats structurés") et le deuxième ne contenant aucune structure physique (appelés "habitats sans structure"). L'objectif de cette étude était de déterminer si le ventre rouge du nord adaptait (i) l'utilisation de la zone littorale en fonction de l'intensité du risque de prédation dans la zone pélagique et (ii) l'utilisation des habitats structurés (relativement aux habitats sans structure) en fonction de l'intensité du risque de prédation dans la zone littorale (Chapitre III).

L'effet de la variation du risque de prédation sur la sélection de l'habitat par le ventre rouge du nord a également été étudié en laboratoire (Chapitre IV). Dans un bassin expérimental, nous avons recréé un système à trois niveaux trophiques, des prédateurs mobiles (le mulet à cornes) s'alimentant sur des proies mobiles (le ventre rouge du nord), ces dernières s'alimentant sur une ressource alimentaire immobile distribuée dans deux habitats distincts. Ces habitats différaient dans la quantité de

ressources disponibles pour la proie, ainsi que dans le risque inhérent à l'habitat (i.e., la complexité structurelle de l'habitat). L'objectif était de déterminer l'importance de la distribution de la ressource alimentaire et du risque inhérent à l'habitat sur la sélection de l'habitat par les proies, lorsque les prédateurs sont libres de se déplacer d'un habitat à un autre.

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CHAPITRE I

SENSITIVITY OF NORTHERN REDBELLY DACE, *PHOXINUS EOS,* TO CHEMICAL ALARM CUES[1]

Angélique Dupuch, Pierre Magnan and Lawrence M. Dill

Angélique Dupuch, Pierre Magnan[2]. Groupe de Recherche sur les Ecosystèmes Aquatiques, Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières (Québec), G9A 5H7, Canada

Lawrence M. Dill. Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby (British Columbia), V5A 1S6, Canada

[1] Dupuch, A., Magnan, P. and Dill, L. M. (2004). This article is published in the Canadian Journal of Zoology, 82, 407-415.

[2] Corresponding author (e.mail: pierre.magnan@uqtr.ca; tel.: 001 819 376 5011 # 3375; fax: 001 819 376-5084)

Résumé

Le ventre rouge du nord, *Phoxinus eos*, est une proie naturelle de l'omble de fontaine, *Salvelinus fontinalis*, dans les lacs du bouclier canadien, en particulier lorsque les individus migrent dans la zone pélagique au coucher du soleil pour se nourrir de zooplancton et que les bancs se dispersent. Les objectifs de cette étude étaient (i) de déterminer si le ventre rouge du nord réagit à des extraits de peau de congénères et a donc le potentiel d'utiliser un système d'alarme chimique pour détecter les prédateurs en nature, (ii) de caractériser la réaction de peur chez le ventre rouge du nord à différentes concentrations de substance chimique d'alerte et (iii) d'estimer l'espace actif de la substance chimique d'alerte chez cette espèce. Les ventres rouges du nord ont répondu à des extraits de peau de congénères par un ensemble de comportements anti-prédateurs: Les individus se rapprochaient du substrat et s'éloignaient de la zone d'injection de la substance chimique d'alerte, augmentaient la cohésion et la polarisation de leurs bancs, et faisaient plus de mouvements brusques et d'immobilisations prolongées. Les réponses observées étaient fortement corrélées à la concentration de la substance chimique d'alerte, suggérant que les individus pourraient utiliser cette sensibilité à différentes concentrations de substance chimique d'alerte pour estimer le risque de prédation en nature. Les expériences de dilution nous ont permis d'estimer que 1 cm^2 de peau de ventre rouge du nord contient suffisamment de substance chimique d'alerte pour générer une réponse des individus dans 110,558 L d'eau, ce qui correspond à un cube de 4.8 m de côtés. Des évidences indirectes suggèrent que le ventre rouge du nord pourrait utiliser les substances chimiques d'alerte pour estimer le risque de prédation par l'omble de fontaine en nature.

Abstract

The northern redbelly dace, *Phoxinus eos*, is subject to predation by brook trout, *Salvelinus fontinalis*, in Canadian Shield lakes, particularly when individuals migrate to the pelagic zone at sunset to feed on zooplankton and fish shoals break up into single individuals. The objectives of the present study were (i) to determine whether northern redbelly dace react to skin extracts from conspecifics and thus potentially use chemical alarm cues to detect predators in nature, (ii) to characterize the fright reaction in northern redbelly dace under different concentrations of alarm substance, and (iii) to estimate the active space of the alarm substance in this species. Northern redbelly dace responded to skin extracts of conspecifics with a series of anti-predator behaviours: they moved closer to the substrate and away from the area where the alarm substance was injected, increased both the cohesion and polarization of their shoals, and performed more dashing and freezing behaviours. The observed responses were closely correlated to the concentration of the skin extract solution, suggesting that individuals could use this sensitivity to different concentrations of alarm substance to estimate the risk of predation in nature. The dilution experiment allowed us to estimate that 1 cm^2 of northern redbelly dace skin contains enough alarm substance to generate a response of individuals in 110,558 L of water, which corresponds to a cube with sides of approximately 4.8 m. Indirect evidence suggests that the northern redbelly dace could use chemical alarm cues to assess the risk of predation by brook trout in nature.

Introduction

Chemical alarm signalling is among the strategies used by fishes to counter predation (Smith 1992) and can be divided into two distinct categories: signals released by prey that are disturbed but not injured, called disturbance signals, and those emitted when the prey is captured by a predator, called damage-released alarm cues (Chivers and Smith 1998). There are numerous examples of damage-released alarm cues in different groups, and especially in ostariophysians (reviews by Pfeiffer 1977; Smith 1992; Chivers and Smith 1998). "Schreckstoff," a term used specifically for ostariophysians (Von Frisch 1938, 1941) and, more generally, alarm substances (also called alarm pheromones) are chemical compounds localized in club cells of the epidermis and released into the water after mechanical damage of the skin, e.g., after a predator attack (Smith 1992). When these alarm substances are detected by nearby conspecifics or other fish species (i.e., cross-species response), they elicit a set of anti-predator behaviours including increased school cohesion and predator inspection, dashing, freezing, looking for shelter, and decreased foraging (Mathis and Smith 1993; Brown and Smith 1997; Chivers and Smith 1998; Nordell 1998; Chivers et al. 2000; Bryer et al. 2001; Mirza et al. 2001; Mirza and Chivers 2003).

The northern redbelly dace, *Phoxinus eos*, is subject to predation by brook trout, *Salvelinus fontinalis*, in Canadian Shield lakes (Magnan 1988; Lachance and Magnan 1990; East and Magnan 1991; Lacasse and Magnan 1992). This species exhibits onshore–offshore diel migrations between the littoral and pelagic zones of these lakes (Naud and Magnan 1988; Comeau and Boisclair 1998). The fish swim in shoals in the littoral zone during the day and migrate to the pelagic zone at sunset, where shoals break up into single fish, and then return to the littoral at sunrise (Naud and Magnan 1988). The dace also show a preference for a densely covered habitat rather than a sparsely covered one in the littoral zone during the day (Naud and Magnan 1988). Northern redbelly dace probably migrate to the pelagic zone at sunset to increase feeding efficiency on zooplankton. Although brook charr could use

chemical alarm cues in nature (Mirza and Chivers 2003), they are primarily visual foragers (Magnan and FitzGerald 1984). The foraging benefit for individuals remaining in the offshore zone may be offset by an increased predation risk during the daylight hours by brook trout, thus resulting in diel onshore–offshore migrations. Chemical alarm signalling could be particularly important for dace when visual cues are limited, especially when swimming at night in the pelagic zone.

The first objective of the present study was to determine whether the northern redbelly dace react to skin extracts from conspecifics, thus indicating the potential use of chemical alarm cues to avoid predators in nature. The second objective was to characterize the fright reaction of the northern redbelly dace under different concentrations of alarm substance. Most laboratory studies that demonstrated the existence of a chemical alarm cues were based on responses to the presence–absence of a stimulus (i.e., distilled water control vs. skin extracts) and thus did not address whether fish adjust their response in relation to their perceived degree of predation risk. Finally, few studies have attempted to determine the amount of alarm substance released when a predator captures a prey animal (Chivers and Smith 1998). The third objective of the study was thus to estimate the active space of the alarm substance in northern redbelly dace, that is, the volume in which the stimulus concentration exceeds the detection threshold of the receiver (Lawrence and Smith 1989).

Materials and Methods

Experimental fish and holding conditions

Northern redbelly dace were collected with a beach seine in Lake Mastigou (Mastigouche Reserve, Québec, Canada; 46°40′N, 73°20′W) in September 1999 and May 2000. Lake Mastigou also contains brook trout and white sucker, *Catostomus commersonii*. Northern redbelly dace are subject to trout predation in this lake (Lacasse and Magnan 1992).

Dace captured in September 1999 were used for pilot experiments and to collect skin extract (see below) while fish captured in May 2000 were used for experiments, which lasted from 13 June to 18 July. The fish were held in a temperature-controlled, dechlorinated freshwater tank (900 L) under a light:dark regime of 12h:12h. Water quality was tested regularly throughout the study and fish appeared to be in good health. Water temperature was maintained at 14 ± 1°C and fish were fed *ad libitum* once a day with commercial trout pellets (Corey Aquaculture 2.0 GR) plus a food supplement (Tetra-Min Flakes).

Chemical stimuli

We prepared skin extract from six northern redbelly dace (5.54 ± 0.48 cm total length; mean ± SD). As Smith (1973) showed that male fathead minnow (an Ostariophysian) lost all cells containing alarm substance during the breeding season, we used dace captured outside their reproductive season. After killing the fish by a blow to the head (in accordance with the Canadian Council on Animal Care Guidelines), we removed a skin filet from both sides of each fish (total area of skin collected = 18.09 cm^2; determined by planimetry with an image analyzer). Immediately after removal, we placed the skin samples in 100 ml of chilled glass-distilled water. We ground the skin samples with a domestic food grinder for 1 min and filtered the homogenate to remove solid particles. From this initial stock solution, we prepared 5-ml skin extract aliquots of different concentrations (0.01%; 0.1%; 1.0% and 10.0% of the initial solution) with distilled water. These solutions (hereafter called "alarm substance") were frozen immediately after preparation. Preliminary experiments indicated that freezing the alarm substance solution did not alter the fishes' response (see also Waldman 1982).

Experimental set-up and protocol

The experiments took place in a 40-L glass aquarium (35 x 25 x 30 cm depth), filled with 0.5 cm of gravel and 30 L of water, and aerated by an air-stone fixed on

the left side. A plastic tube allowed us to inject the alarm substance (15 ml) near the air stone with a 25-ml syringe from behind a black curtain placed around the aquarium. Fish positions and behaviours were filmed from the top (1.20 m) and the side (0.8 m) of the aquarium by two Hi-8 video cameras (RCA and Sony CCD-TR400) connected to a recording system that allowed us to film experiments for periods of 20 minutes (10 minutes before and 10 minutes after alarm substance injection).

Groups of ten fish (5.46 ± 0.2 cm) were used in each experiment. To allow experimental fish to acclimate to the experimental aquarium, they were first transferred from the 900-L holding tanks to a 40-L glass aquarium (similar to the experimental one) for 24h. These fish were then transferred to the experimental aquarium for 24 hours before the beginning of an experiment. Dace were fed a few hours before the beginning of an experiment so that hunger would not affect their behaviour (Morgan 1988a, b). For each alarm substance concentration, five different groups of fish were tested (giving five replicates per concentration). A fish was used only once in our experiment. We used 10 fish per replicate x five replicates per concentration x five concentrations, for a total of 250 experimental fish. The testing order of the different concentrations was determined randomly in the following order 1.0%, Control, 0.1%, 0.01% and 10.0%. The five replicates of each concentration were done consecutively (one experiment per day). After each experiment, the aquarium was washed and the water changed to minimize the exposure of experimental fish to the alarm substance from the previous trial. We used distilled water (DW) as a control stimulus.

Fish response to the alarm substance

We used six descriptors to quantify fish behaviour before and after injection of the alarm substance: indices of vertical and horizontal position in the aquarium, school cohesion and polarization, and number of dashing and freezing behaviours. Indices of vertical and horizontal position and schooling cohesion and polarization

were measured every 30 seconds while the total numbers of dashing and freezing behaviours were counted for the 20 minutes of the experiment.

Vertical and horizontal indices were calculated following Waldman (1982). The vertical index (V_I) was calculated as:

$$V_I = (+1)\,(N_{TOP}) + (0)\,(N_{CENTER}) + (-1)\,(N_{BOTTOM})$$

where N_{TOP} represents the number of fish in the top third of the aquarium, N_{CENTER} the number in the central third of the aquarium, and N_{BOTTOM} the number in the bottom third. This index can range from +10 (all fish in the top third) to –10 (all fish in the bottom third). The horizontal index (H_I) was calculated as:

$$H_I = (+1)\,(N'_{LEFT}) + (0)\,(N'_{CENTER}) + (-1)\,(N'_{RIGHT})$$

where N'_{LEFT} represents the number of fish in the left third of the aquarium, N'_{CENTER} the number in the central third, and N'_{RIGHT} the number in the right third. The horizontal index can range from +10 (all fish in the left side of the aquarium) to –10 (all fish in the right side of the aquarium).

Schooling cohesion and polarization were calculated following Hezcko and Seghers (1981). A grid divided into 1-cm squares was placed over the TV monitor. The X-Y coordinates of each fish's snout were plotted, and the centroid of the school was determined by calculating the mean X-Y coordinates every 30 seconds of the video tape. The mean distance of individual fish from the centre of the school was used as an index of school cohesion (C_I). A decrease in mean distance to centre of the school indicated an increase in school cohesion. The measure of schooling polarization was obtained by determining the heading of each fish (based on 360°) and calculating the mean heading (Batschelet 1981) for the school. The schooling polarization index (P_I) is the mean deviation of fish from the mean heading. When this index decreased, the schooling polarization increased. Dashing behaviour was

defined as very rapid apparently disoriented swimming, while freezing behaviour was defined as very little movement for more than 30 seconds (Lawrence and Smith 1989). These two behaviours are well known anti-predator behaviours in cyprinid fish (Chivers and Smith 1998).

Active space of alarm substances

The "active space" is the volume in which the concentration of the stimulus exceeds the detection threshold of the receiver (Lawrence and Smith 1989). To estimate the active space, one must first estimate the lowest alarm substance concentration (detection threshold) that initiates a response in a given volume (V = 30 L in our experiments). Then, knowing the surface area of the skin used to prepare the various dilutions (18.09 cm^2) and the volume of alarm substance used in the trials (v = 15 ml in our experiment), it is possible to estimate the surface area of skin per ml (S) that generated a response in the receiver for our experimental set-up. So, the "active space" (volume) of water generated by one cm^2 of skin can be estimated as:

$$\text{Active space} = \frac{V}{S.v}$$

Statistical analyses

For each response variable and alarm substance concentration, we used a Wilcoxon paired-sample test to determine if and for which concentration the differences between pre- and post-stimulus observations were significant. We also used Pearson product-moment correlations to determine if the intensity of the fish responses were related to the alarm substance concentration (dose response). The data on dashing and freezing were Log (X + 1) transformed to fulfill the conditions of normality and homogeneity of residuals (Montgomery and Peck 1982). The correlation analysis was more powerful than the single Wilcoxon paired-sample test because it used all observations of each given response variable and concentration

value as a continuous variable. In both analyses, the sample unit was the trial. Although we recognize this as an important issue, we did not attempt to correct probability values for multiple tests given that the Bonferroni correction can be extremely conservative (Peres-Neto 1999; Moran 2003).

Results

Effects of the alarm substance on fish behaviour

The fish swam freely throughout the aquarium during both the acclimation period and the control treatments (DW). We did not find any significant difference between the pre- and post-stimulus periods for any of the response variables in the DW control treatment (Wilcoxon paired-sample test, $p > 0.05$; Figures 1 to 3), with the exception of the number of dashings, which were significantly higher in the post-stimulus compared to the pre-stimulus periods (Wilcoxon paired-sample test, $p < 0.05$; Figure 3). However, we did not find any significant correlation between the pre-stimulus values and the tested concentration treatments for any of the response variables (Figures 1 to 3, before stimulus; Pearson product-moment correlations: $-0.29 < r < 021$; $p > 0.05$). Based on the measured indices, the fish swam over all the horizontal space (Figure 1) and below the middle depth of the aquarium (Figure 1), in groups with low cohesion and polarization (i.e., in shoals rather than in schools *sensu* Pitcher 1986; Figure 2), and performed few dashing and freezing behaviours (Figure 3).

In contrast, the addition of the alarm substance significantly affected fish behaviour both qualitatively and quantitatively (Figures 1 to 3). Based on the paired-sample tests, both the horizontal and polarization indices were less sensitive to the treatment effects (no significant differences between the pre- and post-stimulus for skin extract concentrations of 0.01%, 0.1%, or 1.0%; Wilcoxon paired-sample test, $p > 0.05$). However, all the response variables were significantly correlated with the

concentration of the chemical stimulus (Figures 1 to 3). Following the addition of the alarm substance, the fish moved toward the bottom (Figure 1; vertical index decreased; $r = -0.72$; $t = 5.03$; $p < 0.001$) and into the right third (Figure 1; horizontal index decreased; $r = -0.68$; $t = 4.47$; $p < 0.001$) of the aquarium (away from the injection site), while reducing the number of movements (Figure 3; number of freezing increased; $r = 0.67$; $t = 4.37$; $p < 0.001$) and swimming more erratically (Figure 3; number of dashing increased; $r = 0.78$; $t = 5.02$; $p < 0.001$) than prior to the injection of the alarm substance. Dashing and freezing behaviours did not occur randomly after the introduction of alarm substance; the fish responded by dashing during the first minutes and then freezing. Furthermore, fish swam in a more cohesive (Figure 2; index of cohesion decreased; $r = -0.76$; $t = 4.25$; $p < 0.001$) and polarized (Figure 2; index of polarization decreased; $r = -0.53$; $t = 2.99$; $p = 0.006$) school following addition of the alarm substance.

Temporal changes in fish behaviour during experiments

For the two most sensitive indices, the intensity (as shown by mean values) and the consistency (as shown by standard deviations) of fish response as well as the time needed to return to the pre-stimulus state were directly related to the concentration of the alarm substance (Figure 4 and 5). The higher the concentration of the skin extract was, the stronger, faster, and more consistent the response was among individuals and the longer it took for them to return to the pre-stimulus index level.

Active space of the alarm substance

The skin extract diluted 1:10,000 still produced a reaction in *Phoxinus eos* for the most sensitive response variables (cohesion and vertical indices and numbers of dashing and freezing behaviours). We thus considered this dilution as the threshold for generating a significant response in our experimental set-up. Since the original stock solution contained 18.09 cm^2 of skin diluted in 100 ml of water, and the stock

solution diluted to 1:10,000 still produced a significant reaction ($S = 18.09*10^{-6}$ cm^2 per ml) when 15 ml were added to aquaria containing 30 L of water, we estimated that 1 cm^2 of northern redbelly dace skin contains enough alarm substance to generate a response in individuals in 110,558 L of water, corresponding to a cube having sides of approximately 4.8 m.

Discussion

Our study showed that the northern redbelly dace responds with a fright reaction to skin extract of conspecifics. Overall, the dace moved closer to the substrate and away from the area where the alarm substance was injected, increased both the cohesion and polarization of their schools, and performed more dashing and freezing behaviours (dashing during the first minutes after the introduction of the alarm substance and then freezing). Von Frisch (1941) observed the same sequence of events when European minnows, *Phoxinus phoxinus*, were exposed to water containing substances from injured minnows: the fish first dashed toward the bottom and then aggregated in a corner of the aquarium. Thus, our results indicate that northern redbelly dace possess a chemical alarm system that could potentially be used to detect cues from injured conspecifics in nature. All these responses are consistent with anti-predator behaviours observed in other species exposed to skin extracts of conspecifics (Chivers and Smith 1998) and with behaviours typically seen when the risk of predation is high (Lima and Dill 1990). A schooling individual that performs dashing behaviours is likely to increase the confusion effect because the predator will have more difficulty focusing on a single individual (Pitcher and Parish 1993). An individual performing dashing is also likely to inform other members of the school of the danger. It is known that schooling fish can gain information about the risk of predation through predator inspection behaviour and the behaviour of other fish (Pitcher 1992; Godin 1997). Northern redbelly dace are usually seen in schools of 50

to ~ 300 individuals in the littoral zone of our study lakes (A. Dupuch and P. Magnan, personal observations). It is thus possible that social facilitation might have played a role in our experiments, as in the field. However, we assumed that this factor did not confound the observed results because it was controlled (i.e. fish density fixed at 10 in all experiments). The anti-predator benefits of schooling are also well known. A more cohesive school structure decreases the probability individual fish are preyed on through a dilution effect and communication among fish (Heczko and Seghers 1981; Pitcher and Parish 1993). The school may also react by adopting an escape behaviour (Chivers et al. 1995). Finally, searching for shelter, as evidenced by dace moving close to the substrate and away from the alarm substance, and freezing are also clear anti-predator behaviours (Brown and Godin 1999).

The dilution experiment showed that the observed responses of northern redbelly dace are closely correlated with the concentration of the skin extract solution. Among the large body of literature on chemical alarm signalling (reviews by Chivers and Smith 1998), the studies that have tested the effect of different skin extract concentrations found a positive correlation between the alarm substance dose and the intensity of the fright reaction (Gandolfi et al. 1968; Waldman 1982; Lawrence and Smith 1989; Lozada et al. 2000; Hagen et al. 2002; Jachner and Rydz 2002). Irving and Magurran (1997) studied the fright reaction of the European minnow at one skin extract concentration in an aquarium (DW vs. 1 g/L) and two concentrations in a stream channel (DW vs. 1 g/L and 10 g/L). They observed that the magnitude of the response to skin extract was lower in the stream channel than in the aquarium and, even though the response persisted for slightly longer following exposure to the higher concentration, this difference was not significant. However, it is possible that dilution in the stream channel, which had about 30 times more water than the aquarium, reduced the fishes' response to skin extract and the difference between the two concentrations. Taken together, the results of variable concentration experiments from our study and those from the literature indicate that fish species with a chemical alarm system are very sensitive to different concentrations of skin

extract and could potentially use this sensitivity to assess the risk of predation in nature. Some authors have suggested that the intensity of anti-predator behaviours should be proportional to the perceived predation risk level if the risk varies in time and space (Dill and Fraser 1984; Gilliam and Fraser 1987; Tonn et al. 1992). In general, predation risk will be inversely related to distance from the predator (Lawrence and Smith 1989) and thus, in a chemical warning system, concentration could indicate distance. We might expect that prey will respond as if predators were closer with high concentrations of alarm substance (high predation risk) and as if predators were more distant at low concentrations of alarm substance (low risk of predation). Recent studies that have examined the question of graded vs. non-graded responses to alarm cues found that fathead minnows and rainbow trout, *Oncorhynchus mykiss,* show no graded response, but are capable of detecting cues well below their population specific behavioural response thresholds (Brown et al. 2001a, 2001b; Mirza and Chivers 2003). Below this threshold, individuals may exhibit a suite of threat-sensitive trade-offs and/or "covert" (*sensu* Smith 1999) behavioural responses (Mirza and Chivers 2003). Prey that have not responded "overtly" (*sensu* Smith 1999) to lower concentrations might have used this energy for other processes such as foraging or finding mates (Brown et al. 2001a, 2001b; Mirza and Chivers 2003).

There was some variability in the responses to the alarm substance among fish groups, as indicated by the large confidence limits around our response variable means, especially at the lower concentrations (Figures 4, 5). The observed trend towards lower response intensities may be due to variation in individual behavioural response thresholds. Such individual variability in the intensity of responses has been reported in previous studies (Gandolfi et al. 1968; Pfeiffer 1974; Waldman 1982; Brown et al. 2001a; Mirza and Chivers 2003). For example, Gandolfi et al. (1968) found variations in individual thresholds to alarm substances: while all fish detected the alarm substance at high concentrations, only a minority of these reacted at low concentrations. This variation in an individual's detection threshold may be due to a

variety of factors such as past experience, sex, condition, age, habitat characteristics (Kats and Dill 1998), foraging motivation, parasite load, reproductive state, perceived predation risk, and others. In our study, observed variation in the responses to alarm substance at low concentration may be due to a mixture of "overt" and "covert" behavioural responses (*sensu* Smith, 1999), depending on the individual's detection threshold (e.g. Brown et al. 2001a; Mirza and Chivers 2003). Further experiments will be required to test this hypothesis.

The dilution experiment also allowed us to determine that 1 cm^2 of northern redbelly dace skin contains enough alarm substance to generate a response in 110,558 L of water. Gandolfi et al. (1968) found an active space of ~ 10,000 litres/cm^2 of skin in zebra danio, *Brachydanio rerio,* Lawrence and Smith (1989), a value 58,823 litres/cm^2 of skin in fathead minnow, *Pimephales promelas,* while Mirza and Chivers (2003), values between 135,246 and 270,491 litres/cm^2 of skin in rainbow trout. These estimates are certainly useful to compare the sensitivities of different species detecting alarm substances in the laboratory. However, they give only a crude estimation of the potential of alarm substances in the field because many other factors may come into play, like water movements, physico-chemical characteristics, and the severity of skin damage.

This raises the question of the real use of chemical alarm systems by fish in nature. Surprisingly, the first observation of chemical alarm cues in fish, by Von Frisch (1938), was made in the field. Some studies have provided evidence that fish avoid minnow traps or areas labelled with skin extracts (Mathis and Smith 1992; 1993; Wisenden et al. 1994, 1995; Chivers et al. 1995; Brown and Godin 1999; Gliwicz and Dawidowicz 2001; Mirza and Chivers 2001; Pollock et al. 2003). Recent studies have shown that predator-naïve charr were better able to evade predators if they were previously exposed to alarm signal, thus suggesting a survival benefit to receivers (Mirza and Chivers 2001, 2003). For example, brook charr can learn to recognize predators through releaser-induced recognition learning and this learning enhances survival of individuals during encounters with a predator (Mirza and

Chivers 2000). By recognising predators and being able to assess predation risk (using visual and chemical cues), prey fish can exhibit antipredator responses, which may increase survival. Wisenden and Thiel (2002) also showed that minnow alarm substance attracted predators. In this context, the use of alarm substance could be a benefit because of predator attraction and interference (competition, aggression and others) increasing survival chances of prey. Yet, these results remain inconclusive because the skin extract concentration used in these experiments might not correspond to the effective alarm substance concentration released when a prey is injured by a predator. There is some indirect evidence that the northern redbelly dace would find its ability to detect skin extracts of injured conspecifics, as shown in the present study, useful to counter predation by brook trout in the field. Studies done on 69 lakes of the Canadian Shield have revealed that the relative importance of prey fish (mostly northern redbelly dace) in the stomach contents of brook trout was higher in lakes containing creek chub, *Semotilus atromaculatus*, or white sucker, *Catostomus commersonni*, than in lakes containing only brook trout (Magnan 1988; Lachance and Magnan 1990; East and Magnan 1991; Lacasse and Magnan 1992). Although stomach content data are not a measure of predation risk *per se*, these results suggest that the risk of trout predation upon dace is mediated by a third species (chub or sucker) in these lakes. Proulx (1991) provided some evidence that the extent of dace feeding migrations to the pelagic zone were lower in five lakes containing brook trout and white sucker than in five others containing only brook trout, suggesting that northern redbelly dace can perceive different risks of predation in these lakes. As these migrations occur between sunset and sunrise, when visual cues are limited, chemical alarm signalling could thus be particularly important for dace. During the day, Naud and Magnan (1988) observed that dace in the littoral zone exhibit a preference for a densely covered habitat rather than a sparsely covered one. Brown and Godin (1999) suggested that prey assessing both the visual and chemical cues associated with a predator increase the quality of information obtained and consequently reduce their risk of mortality. So, it could be profitable for northern

redbelly dace to use a chemical alarm system even during the day, when fish have visual cues but swim in more complex habitats than the pelagic zone (i.e., plant cover in the littoral zone; Smith 1992).

In conclusion, our study has shown that northern redbelly dace respond to the alarm substance of conspecifics with a set of anti-predator behaviours. The higher the alarm substance concentration, the stronger and longer was the fright reaction, suggesting that dace can perceive different degrees of predation risk and adjust their behavioural response accordingly. Future research will be required to more directly quantify the prey response to conspecifics injured by predators in the field. For example, one could quantify the prey behaviour in field enclosures having different volumes, with and without the chemical stimulus of a hidden predator preying upon a conspecific (i.e., no visual cue), using an underwater camera system like the one used by Marchand et al. (2002).

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Figure captions

Figure 1. Variations of horizontal and vertical indices before (——) and after (------) the introduction of alarm substance at five different concentrations (Control (distilled water), 0.01%, 0.1%, 1.0% and 10.0%). Each data point is the mean of five replicates ± SD. r is the Pearson correlation coefficient with p value. * Significant difference between pre- and post-stimulus observations as determined by a Wilcoxon paired test; $z = -2.02$, $p<0.05$.

Figure 2. Variations of cohesion and polarisation indices before (——) and after (------) the introduction of alarm substance at five different concentrations (Control (distilled water), 0.01%, 0.1%, 1.0% and 10.0%). Each data point is the mean of five replicates ± SD. r is the Pearson correlation coefficient with p value. * Significant difference between pre- and post-stimulus observations as determined by a Wilcoxon paired test; $z = -2.02$, $p<0.05$.

Figure 3. Variations of dashing and freezing numbers before (——) and after (------) the introduction of alarm substance at five different concentrations (Control (distilled water), 0.01%, 0.1%, 1.0% and 10.0%). Values of dashing and freezing are Log (X+1) transformed. Each data point is the mean of five replicates ± SD. r is the Pearson correlation coefficient with p value. * Significant difference between pre- and post-stimulus observations as determined by a Wilcoxon paired test; $z = 2.02$, $p<0.05$.

Figure 4. Temporal change of the cohesion index during experiments at five different alarm substance concentrations (Control (distilled water), 0.01%, 0.1%, 1.0% and 10.0%). Each data point is the mean of five replicates ± SD.

Figure 5. Temporal change of the vertical index during experiments at five different alarm substance concentrations (Control (distilled water), 0.01%, 0.1%, 1.0% and 10.0%). Each data point is the mean of five replicates ± SD.

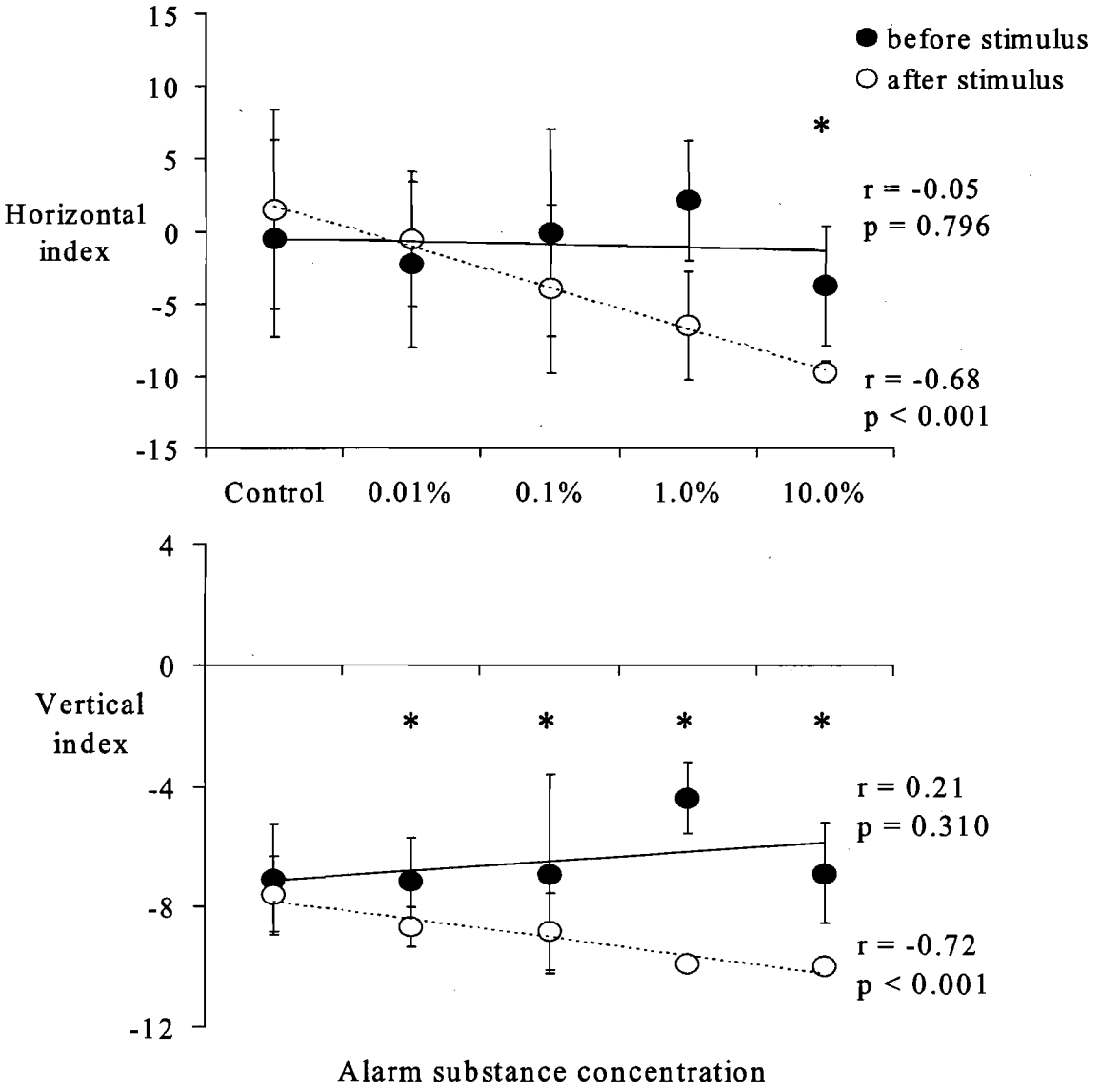
15
10
5
0
-5
-10
-15
Horizontal index
before stimulus
after stimulus
*
r = -0.05
p = 0.796
r = -0.68
p < 0.001
Control
0.01%
0.1%
1.0%
10.0%
4
0
-4
-8
-12
Vertical index
* * * *
r = 0.21
p = 0.310
r = -0.72
p < 0.001
Alarm substance concentration

Figure 1

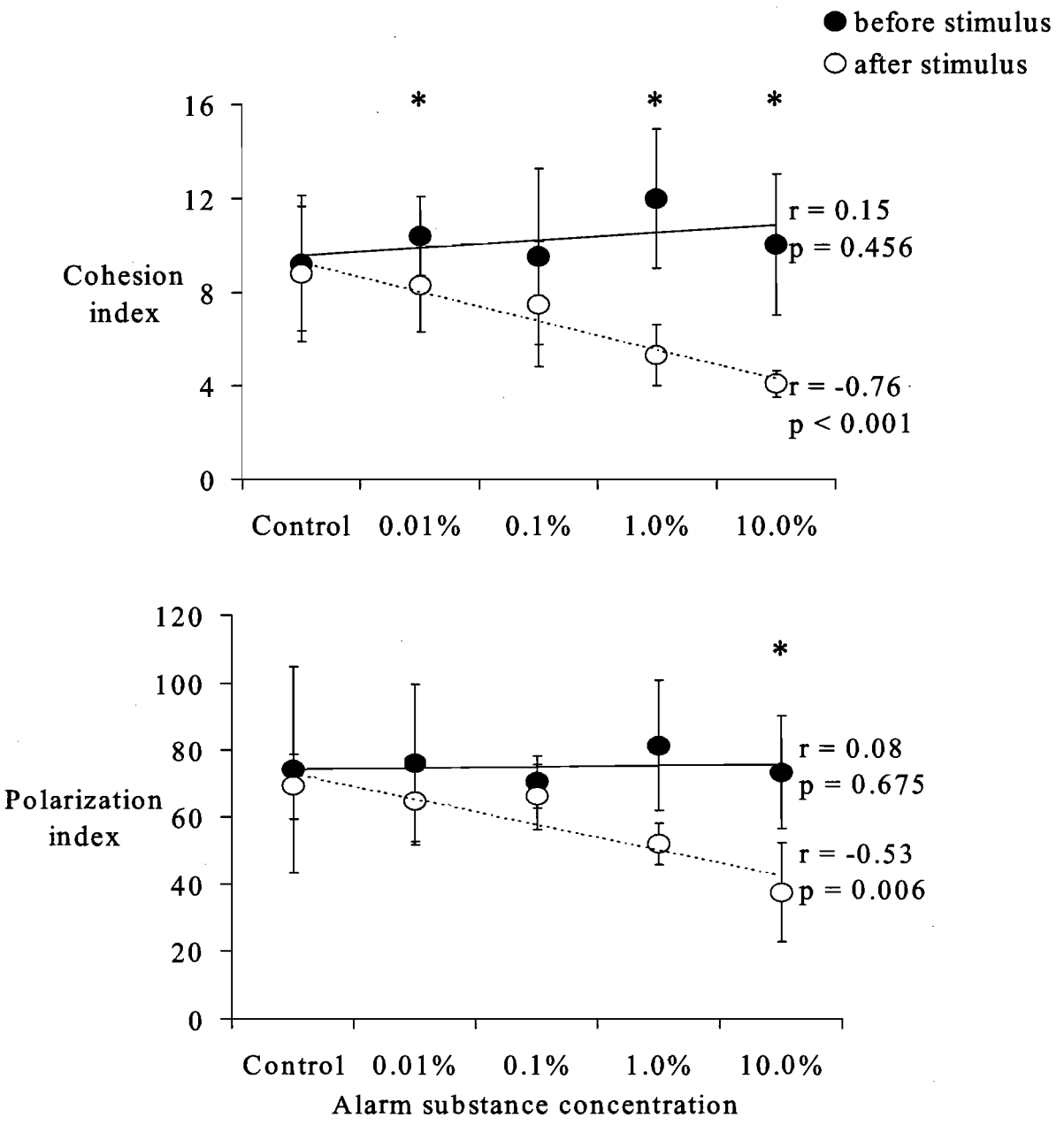
before stimulus
after stimulus
Cohesion index
16
12
8
4
0
*
*
*
r = 0.15
p = 0.456
r = -0.76
p < 0.001
Control
0.01%
0.1%
1.0%
10.0%
Polarization index
120
100
80
60
40
20
0
*
r = 0.08
p = 0.675
r = -0.53
p = 0.006
Control
0.01%
0.1%
1.0%
10.0%
Alarm substance concentration

Figure 2

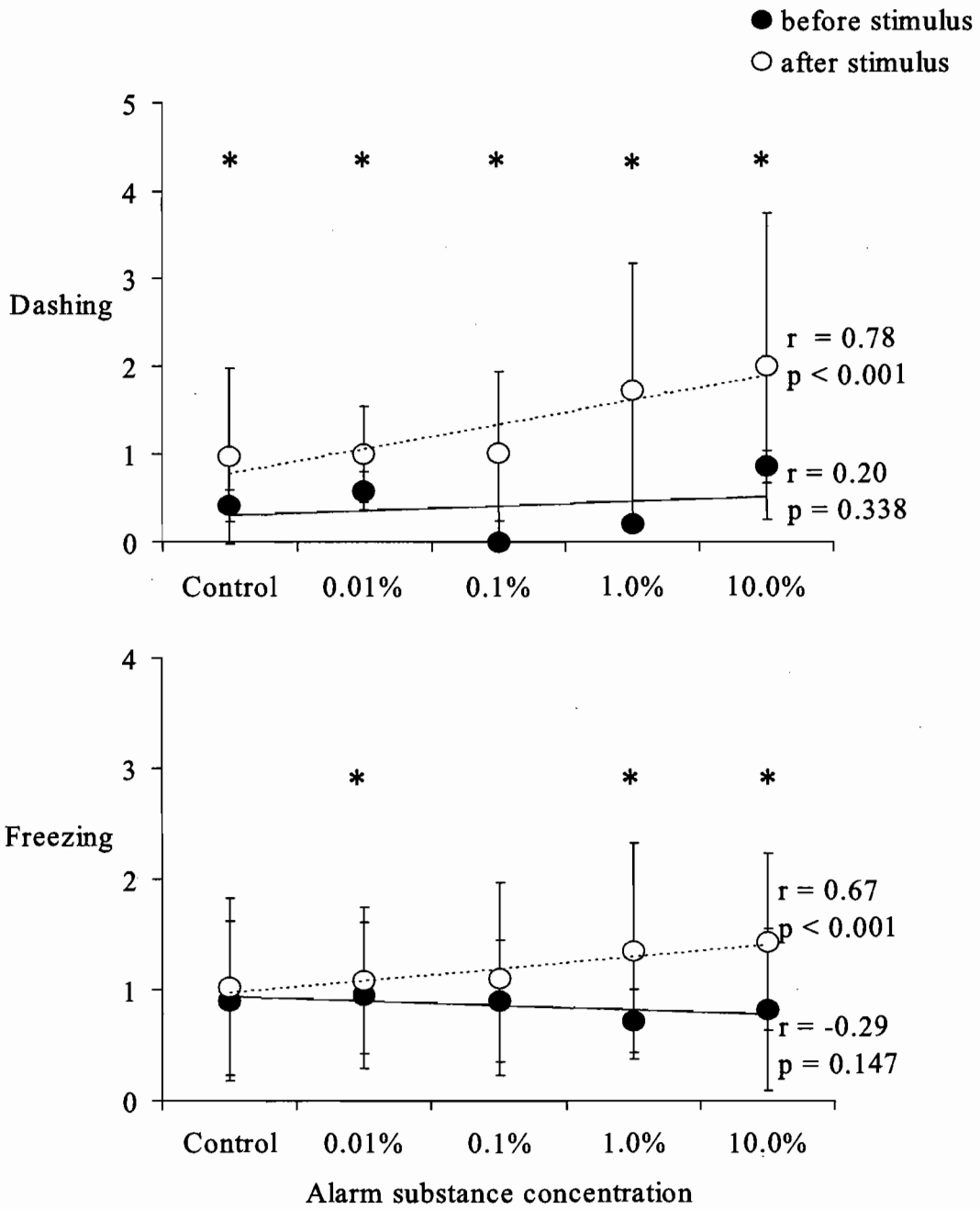
● before stimulus
○ after stimulus
Dashing
5
4
3
2
1
0
*
*
*
*
*
r = 0.78
p < 0.001
r = 0.20
p = 0.338
Control
0.01%
0.1%
1.0%
10.0%
Freezing
4
3
2
1
0
*
*
*
r = 0.67
p < 0.001
r = -0.29
p = 0.147
Control
0.01%
0.1%
1.0%
10.0%
Alarm substance concentration

Figure 3

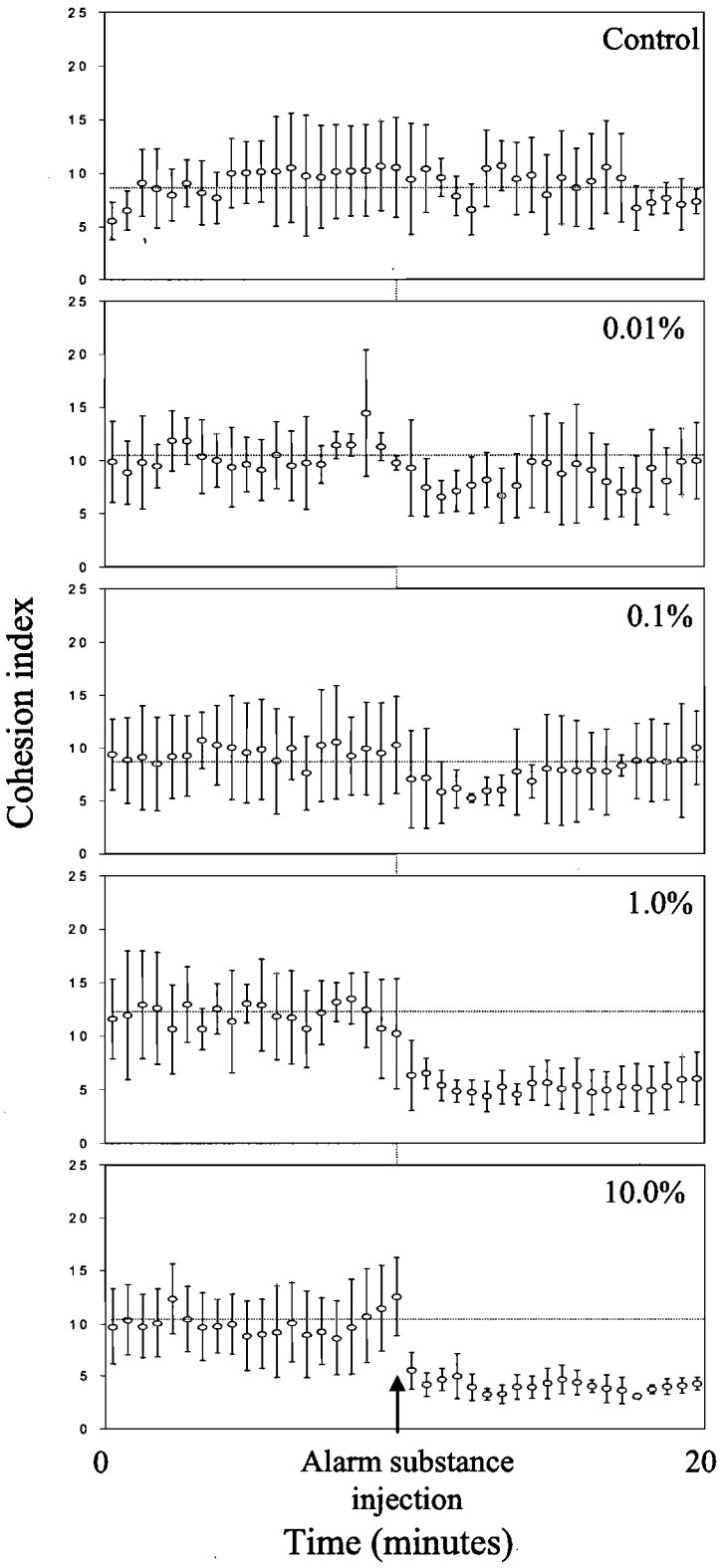
Control
0.01%
0.1%
1.0%
10.0%
Cohesion index
0
5
10
15
20
25
0
Alarm substance injection
20
Time (minutes)

Figure 4

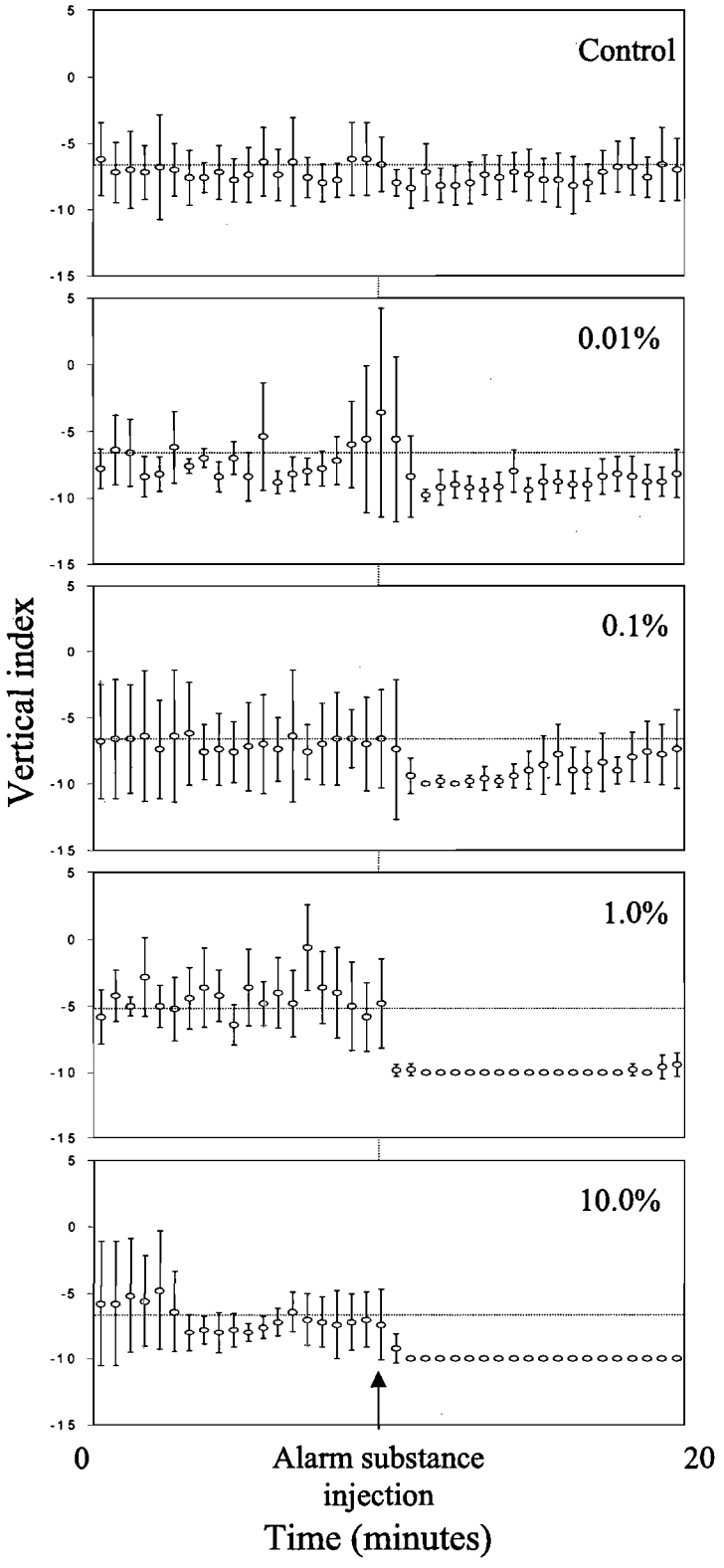
Control
0.01%
0.1%
1.0%
10.0%
Vertical index
5
0
-5
-10
-15
0
Alarm substance injection
20
Time (minutes)

Figure 5

CHAPITRE II

COULD SPATIO-TEMPORAL VARIATIONS IN PREDATION RISK EXPLAIN DIEL HORIZONTAL MIGRATIONS IN NORTHERN REDBELLY DACE?[1]

Angélique Dupuch, Pierre Magnan, Andrea Bertolo and Lawrence M. Dill

Angélique Dupuch, Pierre Magnan[2], Andrea Bertolo. Groupe de Recherche sur les Ecosystèmes Aquatiques, Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières (Québec), G9A 5H7, Canada

Lawrence M. Dill. Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby (British Columbia), V5A 1S6, Canada

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[2] Corresponding author (e.mail: pierre.magnan@uqtr.ca; tel.: 001 819 376 5011 # 3375; fax: 001 819 376-5084)

Résumé

1. Le ventre rouge du Nord, *Phoxinus eos*, effectue des migrations nycthémérales entre les zones littorale et pélagique des lacs du bouclier canadien. Durant la journée, il vit en bancs dans la zone littorale et se disperse dans la zone pélagique durant la nuit pour s'alimenter sur le zooplancton.

2. Si le risque de prédation varie dans le temps et l'espace dans ces lacs, ces migrations pourraient permettre aux ventres rouges du nord de réduire leur risque de prédation par l'omble de fontaine, *Salvelinus fontinalis*, tout en maximisant leur alimentation sur le zooplancton dans la zone pélagique.

3. Nous avons effectué des expériences d'attachement dans 11 lacs pour déterminer (i) les patrons spatiaux et temporels du risque relatif de prédation du ventre rouge du nord lorsqu'il est exposé à la prédation par l'omble de fontaine et (ii) les facteurs déterminant le risque relatif de prédation du ventre rouge du nord.

4. Le risque relatif de prédation était plus élevé dans les zones littorale et pélagique profonde que dans la zone pélagique supérieure et à l'échelle du lac, ne différait pas selon la composition locale de la communauté de poissons.

5. La prédation se déplaçait de la zone pélagique profonde vers les zones littorale et pélagique supérieure dans les lacs où le meunier noir, *Catostomus commersonii*, et/ou le mulet à cornes, *Semotilus atromaculatus*, étaient présents.

6. Le risque relatif de prédation était significativement plus élevé durant la journée que durant la nuit, supportant la notion que l'omble de fontaine est un prédateur visuel.

7. Ces résultats indiquent que le risque relatif de prédation varie dans l'espace (les zones littorale *versus* pélagique supérieure *versus* pélagique profonde) et en fonction de l'intensité lumineuse, et que le mulet à cornes et le meunier noir influencent le patron spatial du risque relatif de prédation mais pas son intensité globale. Les patrons spatiaux et temporels supportent l'hypothèse que les migrations nycthémérales permettraient aux ventres rouges du nord de réduire leur risque de

prédation. Cependant, la persistance de ces migrations dans d'autres systèmes où les prédateurs pélagiques sont absents suggère que d'autres facteurs seraient également impliqués dans l'explication de ces migrations.

Abstract

1. Northern redbelly dace, *Phoxinus eos,* exhibit diel onshore–offshore migrations in Canadian Shield lakes. They form shoals in the littoral zone during the day and disperse in the pelagic zone at night to feed on zooplankton.

2. If predation risk varies in space and time in these lakes, these migrations could allow individuals to reduce their predation risk by brook trout, *Salvelinus fontinalis,* while maximizing foraging on zooplankton in the pelagic zone.

3. We carried out *in situ* tethering experiments in 11 lakes to determine (i) the spatial and temporal patterns of relative predation risk of dace when exposed to trout predation, and (ii) the factors determining the relative predation risk of dace.

4. The relative predation risk of dace was higher in both the mid-pelagic and littoral zones than in the upper-pelagic zone and, at the lake level, did not differ according to the local fish assemblage.

5. Predation events shifted from the mid-pelagic to the upper-pelagic and littoral zones in the presence of non-predatory white sucker, *Catostomus commersonii*, and/or creek chub, *Semotilus atromaculatus*.

6. The relative predation risk was higher during daylight hours than during the night, supporting the notion that the brook trout is a visual predator.

7. These results indicate that relative predation risk varies with spatial location (littoral *versus* upper-pelagic *versus* mid-pelagic zones) and light intensity, and that creek chub and white sucker influence the spatial pattern of relative predation risk but not its overall level. Both spatial and temporal variations in relative predation risk support the hypothesis that diel horizontal migrations allow dace to reduce their predation risk. However, the persistence of these diel migrations in other systems in which pelagic predators are absent suggests that other factors may also play a role in explaining these migrations.

Introduction

Many studies have shown that predators can elicit strong behavioural responses in prey that can reduce their risk of being eaten (Lima & Dill 1990). Fish exhibit numerous anti-predator behaviours, including changes in activity patterns (Gries, Whalen, Juanes & Parrish 1997; Grant & Brown 1998), schooling (Pitcher 1986), and diel migrations between foraging and refuge habitats (Werner & Gilliam 1984; Gibson, Pihl, Modin, Wennhage & Nickell 1998). Habitat use often reflects behavioural decisions associated with foraging, predator avoidance, or reproduction (Sutherland 1996). Since predation risk is not uniform in space or time (e.g., Post, Parkinson & Johnston 1998; Danilowicz & Sale 1999), prey might respond by adapting their spatio-temporal patterns of habitat use. For example, a reduction in brightness, and thus image contrast, can decrease capture rate by visual predators, explaining why many visual predators are not active at night (Benfield & Minello 1996). Thus, prey might use light level as an easily assessable indicator of the risk from visual predators and adjust both their activity levels and habitat use in order to cope with diel variations in predation risk (Clark, Ruiz & Hines 2003; Kronfeld-Schor & Dyan 2003). Helfman (1993) and Reebs (2002) noted that predation risk is an easy *post hoc* explanation for many activity patterns in prey, but that it has seldom been the specific subject of a rigorous study as a possible determinant of a prey's activity patterns. Furthermore, a large number of theoretical predictions in behavioural ecology are based on the notion that the level of predation risk varies in space and time (e.g., Hugie & Dill 1994; Lima & Bednekoff 1999) without having unequivocally determined whether this is the case in nature. Most studies testing these theoretical predictions have been performed in the laboratory or in semi-natural environments (lake enclosures or stream reaches), where it is easy to control the level of predation risk (e.g., Holbrook & Schmitt 1988; Mirza, Mathis & Chivers 2006). In contrast, it is difficult to control predation risk or even to estimate it in nature, and thus to test these theoretical predictions *in situ*.

Northern redbelly dace, *Phoxinus eos,* exhibit diel onshore–offshore migrations in Canadian Shield lakes (Naud & Magnan 1988; Gauthier, Boisclair & Legendre 1997). They form shoals in the littoral zone during the day, disperse in the pelagic zone at sunset to feed on zooplankon, and then return to the littoral zone at sunrise. Similar diel migrations between inshore and offshore zones have been thoroughly studied in coral reef fishes (reviewed in Helfman 1993) and other freshwater species such as roach, *Rutilus rutilus,* (e.g., Gliwicz & Jachner 1992) and golden shiner, *Notemigonus crysoleucas* (Hall, Werner, Gilliam, Mittelbach, Howard & Doner 1979). Although there has been considerable work done on diel migrations (vertical and horizontal), neither the proximal nor the ultimate causes are yet fully understood (Gliwicz 2003). Avoidance of predation risk by piscivorous predators is the function most commonly cited to explain these diel horizontal migrations (hereafter DHM; e.g., Naud & Magnan 1988; Gliwicz & Jachner 1992; Brabrand & Faafeng 1993). However, this hypothesis has never been rigorously tested due to difficulties in measuring predation risk in nature. For instance, Naud & Magnan (1988) suggested that northern redbelly dace use the littoral zone (and especially structured habitats therein) during the day to reduce their predation risk by brook trout, *Salvelinus fontinalis*, a visual predator (Power 1980), and migrate to the pelagic zone at sunset to increase their feeding efficiency on zooplankton. This system is thus a good model to test if predation risk varies in space and time in nature and if these variations are related to changes in prey activity patterns.

Previous studies based on stomach content analysis showed that brook trout prey upon northern redbelly dace (East & Magnan 1991; Proulx 1991; Lacasse & Magnan 1992). Furthermore, the occurrence of northern redbelly dace in the diet of brook trout was higher in lakes containing non-predatory white sucker, *Catostomus commersonii*, and/or creek chub, *Semotilus atromaculatus*, than in lakes containing only brook trout (Lachance & Magnan 1990; East & Magnan 1991; Lacasse & Magnan 1992), suggesting that white sucker and creek chub influence the predation risk of northern redbelly dace by brook trout. The occurrence and frequency of prey

in stomachs have often been used as an index of predation risk (e.g., Salini, Blaber & Brewer 1990; Brewer, Blaber, Salini & Farmer 1995). However, stomach content analysis is not a true measure of predation risk and may give a biased picture of predator–prey interactions. In fact, Magnan, Proulx & Plante (2005) showed that the presence of creek chub and white sucker is correlated with lower abundances of brook trout in oligotrophic Canadian Shield lakes. Consequently, the higher occurrence of northern redbelly dace in the stomachs of brook trout in lakes containing creek chub and white sucker might reflect a shift by trout to pelagic prey in these lakes, even if the overall predation risk of dace may be lower due to a reduced abundance of trout. Because of such mixed effects, it is difficult to relate fish occurrence in stomach contents to predation risk experienced by individual prey.

The tethering technique has been shown to be an effective approach to measure the combined effect of predator abundance and the intensity of their foraging activity (Aronson & Heck 1995; Post *et al.* 1998). This technique provides estimates of relative predation risk since prey avoidance behaviour is eliminated. The objective of our study was to estimate the relative predation risk of northern redbelly dace in lakes containing either brook trout and dace, or brook trout, dace, white sucker and/or creek chub. We conducted tethering experiments in 11 oligotrophic lakes of the Canadian Shield during two consecutive summers to directly assess the relative predation risk of dace in the field. Because we used chronographic tethers (Danilowicz & Sale 1999) at different depths in both the littoral and pelagic zones, it was possible to estimate the spatio-temporal variation in relative predation risk of dace in the different fish communities. We predicted that the relative predation risk of northern redbelly dace would be (i) higher in daylight periods than during the night because the brook trout is a visual predator (Power 1980); (ii) higher in the pelagic than in the littoral zone as the latter is used as a refuge habitat (Naud & Magnan 1988); and (iii) higher in lakes with creek chub and white sucker than in lakes containing only brook trout because trout shift from littoral to pelagic prey when living in sympatry with chub and sucker. Even though trout are overall less abundant

in these latter lakes, their higher occurrence in the pelagic zone compared to lakes without creek chub and white sucker (Tremblay & Magnan 1991) should increase the relative predation risk of dace.

Materials and methods

Study sites

The experiments took place in 11 lakes located in the Mastigouche Reserve, Québec, Canada (46°40′N, 73°20′W), from July 3 to August 27, 2002, and from June 25 to August 22, 2003. These are typical small oligotrophic Canadian Shield lakes with respect to surface area, mean depth and Secchi depth transparency (Table 1). We considered that, besides brook trout, potential piscivores (fish and birds) were negligible in the study lakes. Creek chub is a generalist feeder (Scott & Crossman 1974), with large individuals (total length > 135 mm) feeding on small fish (e.g., Gilliam & Fraser 1987). Given the low abundance of large creek chub in the study lakes (A. Dupuch, personal observation), and the absence of small fish in stomach contents of individuals captured in lakes similar to our study (Magnan & Fitzgerald 1982, 1984), we assumed that this species was a negligible predator for dace. Furthermore, piscivorous birds (common loon, kingfisher and great heron) were rarely observed on the study lakes. So, like for creek chub, we consider their effect on the relative predation risk of northern redbelly dace as negligible compared to brook trout.

Experimental set-up

During the summer of 2002, predation risk in each lake was estimated once in both July and August in the same sequence. In each lake, 72 northern redbelly dace were attached individually to chronographic tethers (Danilowicz & Sale 1999). These were placed at seven different depths in the water column (0.2, 1.0, 2.0, 3.0, 4.0, 5.0

and 6.0 m) at locations above five different isobaths (0.5, 1.0, 2.0, 4.0 and 8.0 m) (Fig. 1A). A total of 1584 individuals were attached to chronographic tethers in 2002 (11 lakes x 2 sampling dates x 18 depth-isobath combinations x 4 prey per combination).

During the summer of 2003, we sampled a subset of seven lakes (Table 1). Each lake was sampled three times during the summer except Lake Gauthier, which was sampled only twice (each set of samples, one per lake, was completed within a one-week period). Thirty northern redbelly dace were attached to chronographic tethers in each lake at five different depths in the water column (0.5, 1.5, 2.5, 3.5 and 4.5 m) and above the 1, 2, 3, 4 and 5 m isobaths (Fig. 1B). A total of 600 dace were attached to chronographic tethers in 2003 (7 lakes x 3 sampling dates x 15 prey per depth-isobath combination x 2 replicates per combination, except that Lake Gauthier was sampled only twice). Based on the preliminary analysis of the 2002 data, we concentrated our efforts on the lake zone situated between the 1 and 5 m isobaths in 2003, so the prey depth-isobath combinations were different for this year (Fig. 1). We therefore analyzed these data separately and used the 2003 results to validate those from 2002.

Fish were collected with minnow traps set in the littoral zone between 8h00 and 14h00. They were attached to chronographic tethers with fishing wire inserted into the musculature under the dorsal fin, allowing individuals to swim freely (Fig. 2A). The length of dace used for the tethering experiment was standardized among lakes for both summers (5.3 ± 0.1 cm in 2002 and 6.0 ± 0.3 cm in 2003). Dace were maintained in a given location by an anchored float (Fig. 2B) and placed in an open area (i.e., without vegetation or woody debris) to avoid entanglement. The chronographic tethers were set between 14h00 and 15h30 and removed the next morning, between 7h30 and 9h00, because a previous study had shown that adult brook trout are mostly active at night, sunset and sunrise while very few were active around midday (Bourke, Magnan & Rodriguez 1996). The positions of chronographic tethers were changed randomly each sampling day within a given lake to take into

account spatial variation in density and activity of predators, thus giving a better estimate of the relative predation risk. A predation event starts the chronometer (when the metal plate is released from the chronographic tether; Fig. 2B. For more details, see Ha 1996; Danilowicz & Sale 1999), thus allowing us to determine the time elapsed between the beginning of an experiment and the predation event (hereafter "survival time"). Before the experiment, we verified in the laboratory that dace cannot escape from the tethering wire or pull the metal plate from the chronographic tether by struggling.

Lake thermal profiles (measurements taken at each meter in the water column) were measured for each experiment. The state of all dace remaining at the end of the experiment (dead or alive) was also noted. A significant proportion of fish were dead at the end of an experiment (see Results section). To determine when this mortality occurred during the experiment, we conducted an additional tethering experiment (hereafter "validation experiment") in 2002 on Lake Lafond. A secondary goal of this experiment was to determine whether a predation event was influenced by the state of the tethered dace (dead or alive). If dead dace were less attractive and/or less detectable for brook trout than live ones, predation events should occur mainly on live tethered prey. So, in this experiment, we noted (i) the state (dead or alive) of uneaten dace attached to the chronographic tether every three hours from 16h00 to 7h00 the next morning, and (ii) the time at which predation events occurred, when applicable. To do so, we removed the chronographic tethers from the water column every three hours, noted the state of the uneaten dace, and put the chronographic tethers back. This handling required less than one minute per tether, and we assumed that it did not affect the prey and predator behaviour.

Statistical analysis

Survival times were analyzed using Cox Proportional Hazards (CPH) regressions (Cox & Oakes 1984), a semi-parametric model commonly used in survival analysis that allows one to study the occurrence and timing of mortality or

predation events. The CPH model takes into account censored data and the non-normal distribution usually observed with survival times (Cox & Oakes 1984). In our study, "censored data" were obtained when a fish was still alive at the end of an experiment (i.e., the fish survived the length of the experiment, so the exact survival time was not known). We used the CPH regression model to assess the effects of independent variables on the survival time of dace. In our analysis, the independent variables used were isobath, prey depth, sampling day and fish community (with and without creek chub and/or white sucker, hereafter called lakes "with competitors" and "without competitors," respectively). The CPH regression model is given by the equation:

$$h\,(t|\,X) = \lambda_0(t)\,exp(\beta_1 x_1 + \beta_2 x_2 \ldots + \beta_i x_i)$$

where $h\,(t|\,X)$ is the hazard function at time t for independent variables $x_1, x_2, \ldots x_i$. The value of $h\,(t|\,X)$, the risk that predation occurs at time t, is the product of two factors: a baseline hazard function, λ_0 at time t, and a linear function of i fixed independent variables x_1, x_2 ...and x_i, where $\beta_1, \beta_2, \ldots \beta_i$ are the coefficients of each independent variable. The function $\lambda_0(t)$, which remains undefined, can be seen as the hazard function for an individual whose independent variables all have values of 0. Because $h\,(t|\,X) = -\ln S(t|\,X)$, where $S(t|\,X)$ is the survival function, a positive coefficient for an independent variable indicates that the relative predation risk increases (i.e., survival decreases) with an increase in the value of this variable while a negative coefficient indicates the reverse.

As a first step, we looked at the average effect of fish assemblage on the relative predation risk considering all the tethering data for each sampling year. As a second step, we looked at the effect of fish assemblage according to the spatial position of the tethered prey. Because of lake morphology, an increase in lake isobath was associated with an increase of depths at which tethered prey could be positioned in the water column. Because isobaths and prey depth were thus confounded, we

analyzed the effects of these variables separately. The effects of fish assemblage and isobath (representing essentially the distance from shore) were tested by using only the tethered prey located in the first two meters of the water column (prey depth < 2 m; hereafter "surface layer" analyses). The effects of fish assemblage and prey depth were tested by using only the tethered prey located in the pelagic zone (isobaths > 2 m) but considering the entire water column (hereafter "pelagic zone" analyses). In 2002, data from the 4 and 8 m isobaths, and in 2003 those from the 3, 4 and 5 m isobaths, were analyzed separately in order to test the effect of fish assemblage on relative predation risk at different depths (Fig. 1).

For each of these analyses (i.e., surface layer and pelagic zone), four CPH regression models were built for each sampling year (Table 2) using one or more of the independent variables and interaction terms (data were nested in lakes). The models were based on hypotheses defined *a priori*: (i) only the spatial position of dace influenced their relative predation risk (models A and E, Table 2), (ii) only fish assemblage influenced relative predation risk of dace (model B, Table 2), (iii) both spatial position and fish assemblage influenced the relative predation risk of dace (models AB and EB, Table 2), and (iv) interactions between spatial position and fish assemblage influenced relative predation risk of dace (models ABC and EBD, Table 2). Since each lake was sampled twice in 2002 (once in July, once in August) and three times over one week in either July or in August in 2003, sampling time was included as a covariable in the analysis to control for its potential effects. In 2003, we removed sampling day from all the analyses because this variable was not important in the explanation of the relative predation risk of northern redbelly dace. The sampling order of the study lakes was such that fish assemblages were sampled alternately in each sampling year. This allowed us to test the effect of fish assemblage without correcting for the sampling order, since the effect of sampling order was controlled in the sampling design. Finally, prey depth and water temperature were highly correlated. The Akaïke Information Criteria (AIC; Burnham & Anderson 2002; see below) showed that models including prey depth rather than water

temperature better explained the relative predation risk of northern redbelly dace, so only prey depth was used in all models.

The model selection was based on the AIC, which is based on the principle of parsimony, helping to identify the model that accounts for the most variation with the fewest variables. In order to allow a quick comparison of the models, we computed the AIC differences (Δ_i) for each candidate model as:

$$\Delta_i = AIC_i - AIC_{min}$$

where AIC_i is the AIC value of model i and AIC_{min} is the smallest AIC value within a given set of models (Burnham & Anderson 2002): the larger the Δ_i, the less plausible the model. Because of the small sample size at the 3 m isobath in 2003, the AIC corrected for small sample sizes (AICc; Burnham & Anderson 2002) was also used for the analysis performed on these data. Since the main result did not differ qualitatively between AIC and AICc, we show only results based on AIC here.

The plausibility of each model (as being the best model) was estimated by calculating the Akaïke weights (w_i) (*sensu* Burnham & Anderson 2002). The Akaïke weights allow one to obtain the relative plausibility of each model and can be interpreted as the weight of evidence in favour of a model being the actual best model for the situation at hand (i.e., given the data available and the *a priori* set of models defined; Burnham & Anderson 2002).

By making an analogy with the concept of confidence intervals (CI) used in parameter estimation, Burnham & Anderson (2002) suggested that a "confidence set of models" can be determined among the available set of *a priori* defined models. This means that a subset of plausible models, and not only the best model, could be retained for inference. A practical way to assess which models should be included in the confidence set is to sum the Akaïke weights until the sum is ≥ 0.95 (Burnham & Anderson 2002). This procedure allows one to acknowledge model uncertainty and focus on more than one plausible hypothesis to explain a given phenomenon. When

more than one model was included in the confidence set of models (i.e., if $w_i < 0.95$), we computed the "model averaged estimates" and the "unconditional standard error" of the independent variables present in the models included in the confidence set by weighting the estimates and the standard error by the Akaïke weights (Burnham & Anderson 2002).

The strength of the relationship between each independent variable and the relative predation risk was assessed as a "risk ratio" (Cox & Oakes 1984). The risk ratio is defined as the change in the probability of a predation event as the variable x_i increases by one unit. The estimate and standard error were then used to compute the risk ratio of each independent variable and its 95% CI. Positive and negative relationships are indicated by risk ratios larger or smaller than 1.0, respectively. When the unit value is not included within the risk ratio CI, the relationship is considered as significant (Quinn & Keough 2002). The further the risk ratio from the value 1.0, the greater the effect of that variable on the relative predation risk of dace.

Finally, to determine whether relative predation risk was higher during daylight than during the night, we estimated the mean relative predation risk (percentage of predation per hour per lake) at each period of the day (afternoon, sunset, night, sunrise, morning) for both summers. For each period, the number of prey potentially available was corrected for the number of predation events that occurred in the preceding period. We then performed a mixed model (MIXED procedure of SAS 9.1.3; 2002 SAS package) with repeated-measures and nested designs (lake was nested into the fish assemblage) on the mean relative predation risk for each sampling year. We estimated the effect of period of the day and the interaction between fish assemblage (0 = without competitors; 1 = with competitors) and period of the day to determine whether the presence of competitors influenced the temporal pattern of predation risk of dace. We then compared mean relative predation risk (regardless of fish assemblage because it had no effect; see Results section) with Bonferroni *post hoc* multiple comparison tests. The relative predation risk was normalized using arcsine square-root transformations of the individual percentages.

Results

Two percent of the tethers (N = 31 in 2002 and N = 16 in 2003) were not considered in the analyses because of entanglement of dace in the wires. Furthermore, 16% of the chronographic tethers (N = 253 in 2002 and N = 96 in 2003) were not activated (i.e., the metal plate did not release from the chronographic tether) even though the dace were no longer attached to the wire. Because we were not sure that a predation event occurred on these tethers, we did not consider them in the analyses (however, the results of statistical analyses were the same when we considered these cases as predation events). Considering all these exceptions, an average of 35% of the tethered northern redbelly dace were preyed upon during the experiments (number of predations: N = 453 in 2002; N = 170 in 2003; Table 3).

Tethering caused the mortality of 64% of the 822 uneaten dace in 2002 and of 58% of the 322 uneaten dace in 2003. The validation experiment conducted in Lake Lafond showed that 86% of this mortality occurred during the first three hours following the attachment of the tethers (from 19h to 22h). Over the first three hours, 26 predation events occurred, leaving 45 out of the 71 dace (23 alive and 22 dead) still attached to the chronographic tethers. Our results show that the percentage of predation on these 45 dace did not differ according to the fish's condition (live or dead tethered dace; $\chi^2 = 1.68$, df = 1, $p > 0.05$, n = 45). Furthermore, there was no significant correlation between the survival rates of uneaten dace and the mean percent of predation in the study lakes (N = 22, r = 0.19, $p > 0.05$ in 2002; N = 20, r = 0.28, $p > 0.05$ in 2003). These results suggest that prey mortality due to the tethering procedure did not bias our estimation of relative predation risk.

Because the temporal pattern of relative predation risk was similar for both sampling years (Table 4), we have illustrated only the results for the summer of 2002 (Fig. 3). Mean relative predation risk decreased significantly during the night (Fig. 3). The presence of competitors did not influence this pattern (Table 4). The results also

suggest that the mid-pelagic zone was the riskiest zone for dace for all periods of the day except at night, when all zones were safe (Fig. 4).

More than one model was included in the confidence set of models for the analyses performed in the surface layer and at the different isobaths (except at the 4 m isobaths in 2002 and 5 m in 2003; Table 5). Regardless of the fish assemblage (i.e., with or without competitors), the relative predation risk was higher in the mid-pelagic (isobath > 2 m; 2 m < prey depth ≤ 6 m) and littoral (isobath ≤ 2 m) zones compared to the upper-pelagic zone (isobath > 2 m; 0 m < prey depth ≤ 2 m) in 2002 and 2003 (Fig. 5). The CPH regression revealed that the effect of isobath on the relative predation risk of dace was significant but weak in 2002 (Table 6) and was not significant in 2003 (Table 6). In 2002, the relative predation risk decreased by 12% for each one-meter increase in the isobath (Table 6, isobath risk ratio = 0.88). The risk ratio also revealed that the effect of prey depth on the relative predation risk of dace was significant at all isobaths for both sampling years. For each one-meter increase in the prey depth, the relative predation risk increased by 2.61 to 4.71 times (Table 6).

When we considered all the tethering data without considering their spatial distribution, fish assemblage did not significantly affect the relative predation risk of dace in either sampling year (2002: risk ratio = 1.04, 95% CI = 0.66-1.63; 2003: risk ratio = 1.58, 95% CI = 0.84-2.94). However, surface layer and pelagic zone analyses showed that fish assemblage had a significant effect on the spatial pattern of relative predation risk. The relative predation risk was higher in the mid-pelagic zone of lakes without competitors than with competitors but was lower in the upper-pelagic zone of lakes without competitors than with competitors (Fig. 5, Table 6; [prey depth x fish assemblage] interaction term significant). The relative predation risk also tended to be higher in the littoral zone of lakes with competitors compared to lakes without competitors for both sampling years (Fig. 5). The CPH regressions revealed that relative predation risk near the water surface (prey depth < 2 m) was on average 1.4

and 6.4 times higher for dace in lakes with competitors than without competitors in 2002 and 2003, respectively (Table 6). This fish assemblage effect was significant at all isobaths in 2003 (Table 6; [isobath x fish assemblage] interaction term not significant) but was stronger in the littoral zone than in pelagic zone in 2002 (Table 6; [isobath x fish assemblage] interaction term significant).

Discussion

Our study showed that both spatial location and fish species composition were determinants of the relative predation risk of northern redbelly dace. The relative predation risk of dace was the lowest in the upper-pelagic zone compared to the mid-pelagic and littoral zones in both fish assemblages. The relatively lower abundance of brook trout in this zone likely explains this result. Brook trout have been found to be significantly more abundant in the lower than in the upper part of the water column (Tremblay & Magnan 1991). Similarly, Bourke *et al.* (1996) also found that brook trout remain in water of about 12°C during the daylight period, which corresponds to depths between 4 and 6 m based on our temperature profiles. Furthermore, brook trout feed preferentially on benthic prey, which are mainly found in the littoral zone, leading to a higher abundance of brook trout in the littoral than in the upper-pelagic zone (Tremblay & Magnan 1991).

Contrary to our expectations, the relative predation risk on dace was on average comparable in lakes containing creek chub and/or white sucker and in lakes containing only brook trout (lakes with competitors and lakes without competitors, respectively). Since the abundance of brook trout is lower in lakes with competitors than without competitors (Magnan *et al.* 2005), this result suggests that brook trout exhibit a more active piscivorous behaviour when living with creek chub and/or white sucker, supporting previous results based on stomach content data (East & Magnan 1991; Lacasse & Magnan 1992). Moreover, the piscivory of brook trout was not

spatially homogeneous between fish assemblages: we observed an increase in predation events in the upper-pelagic zone but a decrease in the mid-pelagic zone in lakes with competitors compared to lakes without competitors. This change was apparent from the littoral zone to the 5 m isobath but not at the 8 m isobath (Fig. 5). The results of Magnan & Fitzgerald (1982) and Tremblay & Magnan (1991) showed that brook trout shifted their spatial distribution from the bottom to the upper part of the water column in the presence of creek chub and white sucker. Thus, our results could reflect the cumulative effects of creek chub and white sucker on the spatial distribution of brook trout. That this change in the spatial distribution of predation events was not observed at the 8 m isobath may be because the effect of chub and sucker decrease with distance from the littoral zone. Tremblay & Magnan (1991) showed that brook trout reduce their use of the littoral zone in response to competition by white sucker. This contrasts with our results, which showed that the relative predation risk in the littoral zone tended to be higher in lakes with competitors than without competitors for both years. Creek chub occurs mainly in the littoral zone (Magnan & Fitzgerald 1982; Magnan & Fitzgerald 1984). Gillnet sampling showed that creek chub are not found beyond the 3 m isobath in our study lakes (unpublished data). This suggests that, contrary to our assumption, predation by creek chub could partly contribute to the higher relative predation risk of dace in the littoral zone of lakes. Since tethering impeded avoidance behaviour, it could be possible that dace were extremely easy prey even for chub.

Our results confirm that light intensity is also a determinant of the predation risk of dace. Relative predation risk was very low during the night compared to daylight hours regardless of fish assemblage. The mean relative predation risk was underestimated in the sunset, night, sunrise and morning periods because we did not replace the tethered dace after each of these. However, the fact that the mean relative predation risk significantly decreased after sunset and significantly increased at sunrise clearly indicates that predation risk of dace was the lowest during night. This low relative predation risk during the night suggests that even if prey are outside their

shelter, the light intensity is too low to allow brook trout to detect and capture them. This supports the hypothesis that light intensity is an important determinant of predation risk for visually oriented predators such as brook trout, as assumed in the concept of an "antipredator window" (Clark & Levy 1988). Furthermore, our lakes differed in their mean relative predation risk, in their fish assemblage, and likely also in their brook trout densities. Despite this, similar temporal patterns of predation risk were found in both fish assemblages, suggesting that temporal patterns of brook trout behaviour and activity were qualitatively the same with or without competitors.

If DHM allows dace to reduce their predation risk by brook trout, we would expect that the relative predation risk would be lowest in the littoral zone during daylight hours. Our results showed that the littoral zone was on average safer for dace than the mid-pelagic zone but riskier than the upper-pelagic zone during the daylight hours. However, our study probably overestimated the relative predation risk in the littoral zone because (i) chronographic tethers were not installed in the vegetation for logistical reasons, (ii) dace preferentially use shallow vegetated areas in the littoral zone of lakes (Naud & Magnan 1988; He & Lodge 1990; Jacobus & Ivan 2005), and (iii) the structurally complex habitats of the littoral zone offer shelter for prey fish both by hindering the visual detection of prey by predators and by reducing the predator's foraging ability (Savino & Stein 1982). East & Magnan (1991) showed that the presence of refuge (macrophyte beds) significantly reduced the number of attacks and captures of northern redbelly dace by brook trout in laboratory experiments. Although we do not know the importance of creek chub predation to the overall risk of dace, we would expect that the safest zone for dace during daylight hours would be the littoral zone, due to the presence of vegetated habitats. Therefore, based on the spatio-temporal pattern of predation risk, avoidance of predation would explain the use of the littoral zone during the day and of the upper-pelagic zone at night. Indeed, Naud & Magnan (1988) showed that, in a lake of Mastigouche Reserve containing brook trout, more than 80% of dace captured in the pelagic zone between sunset and sunrise were in the upper-pelagic zone. Given that dace had more than a

50% chance of being preyed upon by trout below 3 m depth in the water column (Fig. 5), we suggest that dace adapted their vertical distribution to avoid such risky depths while feeding on zooplankton in pelagic zone.

DHM has also been observed in the absence of predators (e.g., in *Phoxinus* sp.: Gaudreau & Boisclair 1998; in *Rutilus rutilus*: Jacobsen & Perrow 1998). This questions the importance of predation risk in determining DHM and suggests that other hypotheses could explain it. First, DHM may be genetically fixed (Gliwicz & Jachner 1992; Mehner, Kasprzak & Hölker 2007) and could persist even when the evolutionary pressure that may have been responsible for its development is relaxed. DHMs persist because prey fish respond to proximate factors such as light intensity and the habitat's structural complexity, even in the absence of predators. Second, as suggested by Gaudreau & Boisclair (1998), habitat profitability may switch from the littoral zone during the day to the pelagic zone at night because of an upward migration and concentration of zooplankton at the surface of the pelagic zone. This supposes that the causative mechanism of DHM is a maximization of food intake (and subsequent growth rate) and not predator avoidance. Third, migrations from the pelagic to the littoral zone could be driven by water temperature, since moving from cooler to warmer water speeds up metabolism and growth as long as sufficient food is available (Neverman & Wurstsbaugh 1994; Garner, Clough, Griffiths, Deans & Ibbotson 1998). It could thus be hypothesized that after feeding on zooplankton in the pelagic zone at night, dace return to the warmer water of the shallow littoral zone during the day because of a bioenergetic advantage, as shown in *Phoxinus phoxinus* in a river habitat (Garner *et al.* 1998). The three general hypotheses of predator avoidance, foraging opportunity, and bioenergetic efficiency, are not mutually exclusive and can explain the diel migrations (vertical and horizontal) observed in many fish species (see references in Introduction). A combination of these factors probably controls the timing and amplitude of these diel migrations. Furthermore, the relative importance of each mechanism likely depends on predation vulnerability,

degree of hunger (and satiation), and the metabolic demand of individuals in each zone (littoral *versus* pelagic).

In conclusion, our study showed that spatial location, fish assemblage and light intensity were important determinants of the relative predation risk for northern redbelly dace. Furthermore, spatial and temporal patterns of relative predation risk support the hypothesis that diel horizontal migrations allow dace to reduce their predation risk by brook trout by migrating to the pelagic zone to feed on zooplankton at night, when risk from visual predators is reduced. However, the fact that northern redbelly dace perform diel horizontal migrations in the absence of pelagic predators suggests that other mechanisms are also involved in explaining this behaviour.

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Table 1: General characteristics and fish composition of the study lakes. Pe = *Phoxinus eos*; Sf = *Salvelinus fontinalis*; Cc = *Catostomus commersonii*; Sa = *Semotilus atromaculatus*

Lake	Surface area (ha)	Maximum depth (m)	Secchi depth (m)	Pe	Sf	Cc	Sa	Sampling 2002	Sampling 2003
Bondi	25.7	29.3	4.3	✔	✔			✔	✔
Cerné	13.2	9.3	3.5	✔	✔			✔	✔
Diablos	9.8	16.5	4.9	✔	✔			✔	
Lafond	46.7	23.3	5.5	✔	✔			✔	✔
Osborn	10.8	12.8	5.8	✔	✔			✔	✔
Joe	25.6	13.0	5.8	✔	✔	✔		✔	
Gauthier	36.9	21.4	4.2	✔	✔		✔	✔	✔
Lafleur	21.8	19.0	7	✔	✔		✔	✔	
Grignon	29.6	21.0	6.3	✔	✔	✔	✔	✔	✔
Grosse	8.0	17.0	3.5	✔	✔	✔	✔	✔	✔
Tête	23.1	18.0	4.1	✔	✔	✔	✔	✔	

Table 2: Set of candidate models based on four hypotheses defined *a priori* to explain the relative predation risk of dace in the study lakes. See text for details.

Model	Variables
2002	
surface layer	
A	isobath + sampling month
B	fish assemblage. + sampling month
AB	isobath + fish assemblage + sampling month
ABC	isobath + fish ass. + sampling month + isobath x fish ass.
isobaths 4 m and 8 m	
E	prey depth + sampling month
B	fish assemblage+ sampling month
EB	prey depth + fish assemblage + sampling month
EBD	prey depth + fish ass.+ sampl. month + prey depth x fish ass.
2003	
surface layer	
A	isobath
B	fish assemblage
AB	isobath + fish assemblage
ABC	isobath + fish assemblage + isobath x fish assemblage
isobaths 3 m, 4 m and 5 m	
E	prey depth
B	fish assemblage
EB	prey depth + fish assemblage
EBD	prey depth + fish assemblage + prey depth x fish assemblage

Table 3: Number of tethered fish and mean percent predation ± SD in the study lakes in 2002 and 2003. Percent predation was estimated as the mean percent of missing dace after one sampling day (mean is based on two sampling days in 2002 and three in 2003).

Fish assemblage	Lake	Number of tethered fish		Mean percent predation ± SD	
		2002	2003	2002	2003
Without competitors					
	Bondi	110	78	38 ± 13	28 ± 6
	Cerné	124	68	40 ± 3	39 ± 15
	Diablos	120		46 ± 5	
	Lafond	126	81	23 ± 5	17 ± 4
	Osborn	120	82	22 ± 21	32 ± 10
	Average			34 ± 11	29 ± 9
With competitors					
	Joe	134		25 ± 5	
	Lafleur	106		43 ± 18	
	Gauthier	109	50	46 ± 24	17 ± 18
	Grignon	112	63	23 ± 2	53 ± 17
	Grosse	94	70	55 ± 9	50 ± 28
	Tête	117		27 ± 7	
	Average			37 ± 13	40 ± 20
All lakes				35 ± 12	34 ± 14

Table 4: Results of the mixed models performed on the data from 2002 and 2003 to determine the effects of period of the day (afternoon, sunset, night, sunrise and morning) and fish assemblage (0 = without competitors; 1 = with competitors) on the mean relative predation risk.

	Variables	df	F-value	P-value
2002				
	Day period	4/36	15.61	< 0.001
	Fish assemblage	1/9	0.04	0.847
	Day period x fish assemblage	4/36	0.72	0.583
2003				
	Day period	4/20	5.65	0.003
	Fish assemblage	1/5	0.37	0.568
	Day period x fish assemblage	4/20	0.62	0.651

Table 5: Results of the model selection based on the Akaïke information criterion (AIC) for years 2002 and 2003. The number of parameters used in the model (k), AIC, AIC differences (Δ_i) and Akaïke weights (w_i) are shown (see text for details on statistical analyses). Bold indicates models included in the 95% confidence set of models based on w_i.

Model		k	AIC	Δ_i	w_i
2002					
surface layer	A	4	2135.3	2.3	**0.14041**
	B	4	2135.0	2	**0.15991**
	AB	5	2133.0	0	**0.43469**
	ABC	6	2134.0	1	**0.26497**
isobath 4 m	E	4	1158.3	13.6	0.00112
	B	4	1210.8	66.1	0.00000
	EB	5	1152.3	7.6	0.02175
	EBC	6	1144.7	0	**0.97712**
isobath 8 m	E	4	2443.7	0	**0.64568**
	B	4	2619.1	175.4	0.00000
	EB	5	2445.7	2	**0.23753**
	EBC	6	2447.2	3.5	**0.11678**
2003					
surface layer	A	3	471	33.2	0.00000
	B	3	437.8	0	**0.66412**
	AB	4	439.8	2	**0.24554**
	ABC	5	441.8	4	**0.09033**
isobath 3 m	E	3	199.1	4.8	**0.05499**
	B	3	200.9	6.6	0.02235
	EB	4	195.6	1.3	**0.31645**
	EBD	5	194.3	0	**0.60619**
isobath 4 m	E	3	470.3	2	**0.23226**
	B	3	504.2	35.9	0.00000
	EB	4	471.5	3.2	**0.13004**
	EBD	5	468.3	0	**0.63769**
isobath 5 m	E	3	552.7	27	0.00000
	B	3	590.2	64.5	0.00000
	EB	4	547.9	22.2	0.00001
	EBD	5	525.7	0	**0.99998**

Table 6: Model-averaged estimate, unconditional standard error, risk ratio and 95% confidence interval for variables included in the selected models (see Table 5) in 2002 and 2003. Bold indicates variables that were important to explain the relative predation risk of dace (see text for details).

	Variable	Estimate (±SE)	Risk ratio	95% CI
2002				
surface layer	**Isobath**	**-0.13(0.06)**	**0.88**	**0.78-0.99**
	Fish assemblage	0.32(0.31)	1.38	0.75-2.50
	Sampling month	**-0.65(0.23)**	**0.52**	**0.33-0.81**
	Isobath x fish assemblage	**-0.17(0.09)**	**0.84**	**0.71-0.99**
isobath 4 m	**Prey depth**	**1.05(0.11)**	**2.85**	**2.24-3.56**
	Fish assemblage	-0.21(0.31)	0.81	0.44-1.46
	Sampling month	**-0.81(0.24)**	**0.44**	**0.27-0.71**
	Prey depth x fish assemblage	**-0.61(0.21)**	**0.54**	**0.36-0.82**
isobath 8 m	**Prey depth**	**0.96(0.10)**	**2.61**	**2.16-3.19**
	Fish assemblage	0.03(0.09)	1.03	0.87-1.23
	Sampling month	-0.16(0.30)	0.85	0.47-1.53
	Prey depth x fish assemblage	-0.12(0.18)	0.88	0.62-1.26
2003				
surface layer	Isobath	0.02(0.07)	1.02	0.89-1.16
	Fish assemblage	**1.86(0.51)**	**6.42**	**2.36-17.51**
	Isobath x fish assemblage	-0.02(0.34)	0.98	0.50-1.91
isobath 3 m	**Prey depth**	**0.98(0.43)**	**2.66**	**1.15-6.20**
	Fish assemblage	**1.36(0.64)**	**3.89**	**1.12-13.60**
	Prey depth x fish assemblage	**-0.96(0.36)**	**0.38**	**0.19-0.77**
isobath 4 m	**Prey depth**	**1.09(0.23)**	**2.97**	**1.90-4.64**
	Fish assemblage	0.61(0.34)	1.84	0.94-3.59
	Prey depth x fish assemblage	**-0.72(0.28)**	**0.48**	**0.28-0.86**
isobath 5 m	**Prey depth**	**1.55(0.14)**	**4.71**	**3.59-6.11**
	Fish assemblage	0.13(0.56)	1.13	0.38-3.35
	Prey depth x fish assemblage	**-1.48(0.29)**	**0.22**	**0.12-0.40**

Figure captions

Figure 1: Positions of chronographic tethers in the study lakes in 2002 and 2003. Four chronographic tethers in 2002 and two in 2003 were placed at each prey depth-isobath combination.

Figure 2: (a) Chronographic tether mechanism with metal plate (1), 15-cm tethering line (2) and attached prey (3) (adapted from Danilowicz and Sale 1999). (b) Experimental set-up showing the method for positioning the chronographic tether and fish in the water column. The device was maintained at a given position in the lake with an anchor.

Figure 3: Box plots representing the variation in mean relative predation risk on northern redbelly dace at different periods of the day (from 14h00 to 7h30) for lakes with brook trout only (grey bars) and with brook trout and competitors (white bars) during the summer of 2002. Each box plot shows the middle quartiles and the horizontal line in the middle of the box marks the median. The edges of each box (hinges) mark the 25 and 75^{th} percentiles. The length of the box corresponds to the interquantile range (IQR). The whiskers show the range of values that fall within 1.5 IQR of the hinges. Outliers (value between 1.5 and 3 IQR outside of the hinges) are marked by an asterisk. The sunset and sunrise periods were defined as one hour before to one hour after sunset and sunrise, respectively. Sunset and sunrise times were found in the sunrise/sunset tables given by the National Research Council of Canada for Trois-Rivières (Québec, Canada). Mean relative predation risks (regardless of fish assemblage) with different letters were significantly different ($p < 0.010$).

Figure 4: Box plots representing the variation in mean relative predation risk on northern redbelly dace at different periods of the day (from 14h00 to 7h30) in the

littoral zone (isobath < 2 m; white bars), in the upper-pelagic zone (isobath > 2 m; prey depth < 2 m; grey bars) and in the mid-pelagic zone (isobath > 2 m; prey depth > 2 m; dark bars) during the summer of 2002. See Fig. 3 for description of box plot. Circles represent extreme values (more than 3 IQR outside hinges).

Figure 5: Mean percent predation (represented by the width of circle) in lakes without and with competitors for each prey depth-isobath combination for the summers of 2002 and 2003. Percent predation was estimated as the mean percent of missing dace after one sampling day (mean for lakes without competitors is based on six and four lakes in 2002 and 2003, respectively; mean for lakes with competitors is based on five and three lakes in 2002 and 2003, respectively).

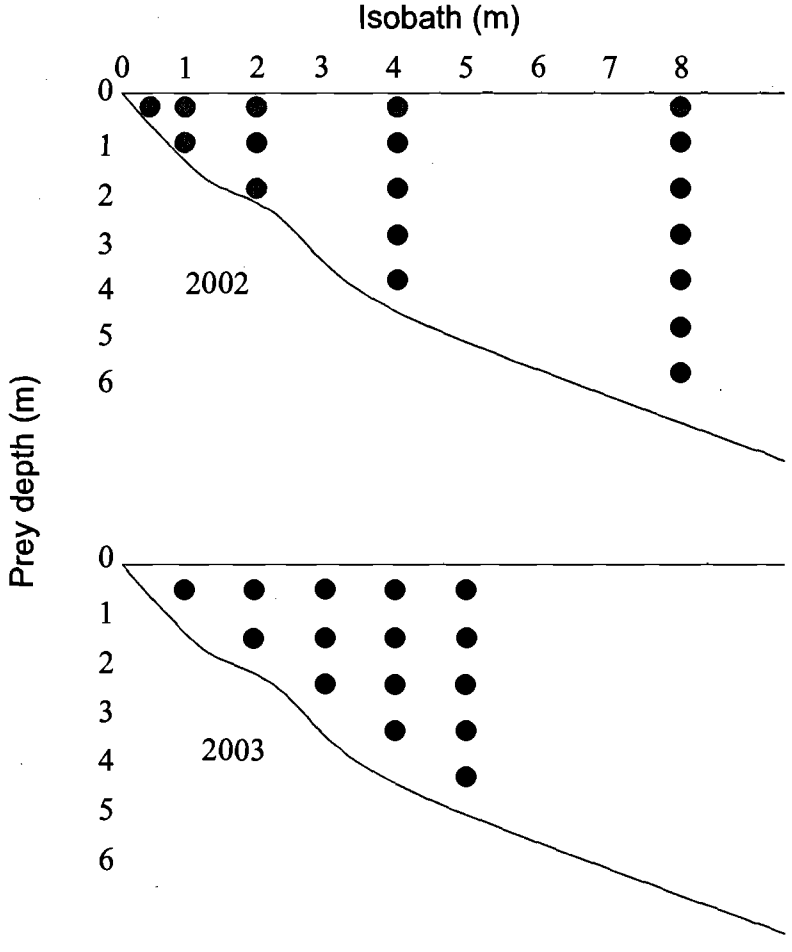

Figure 1

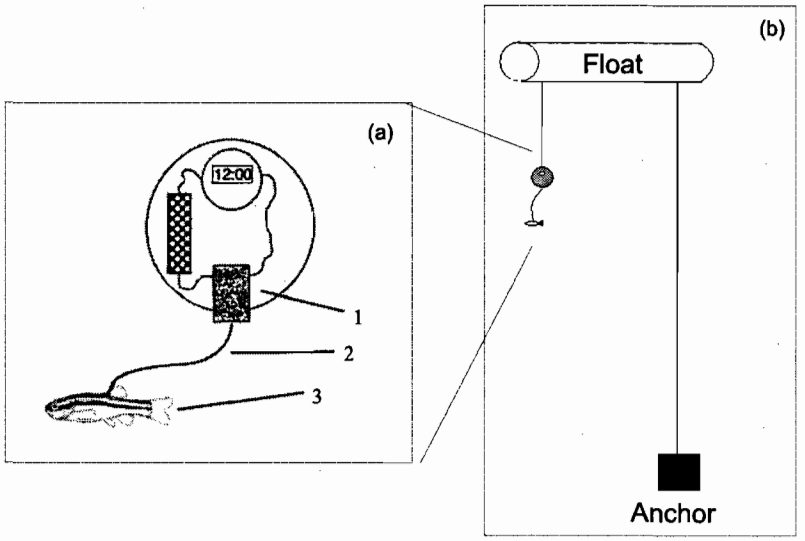

Figure 2

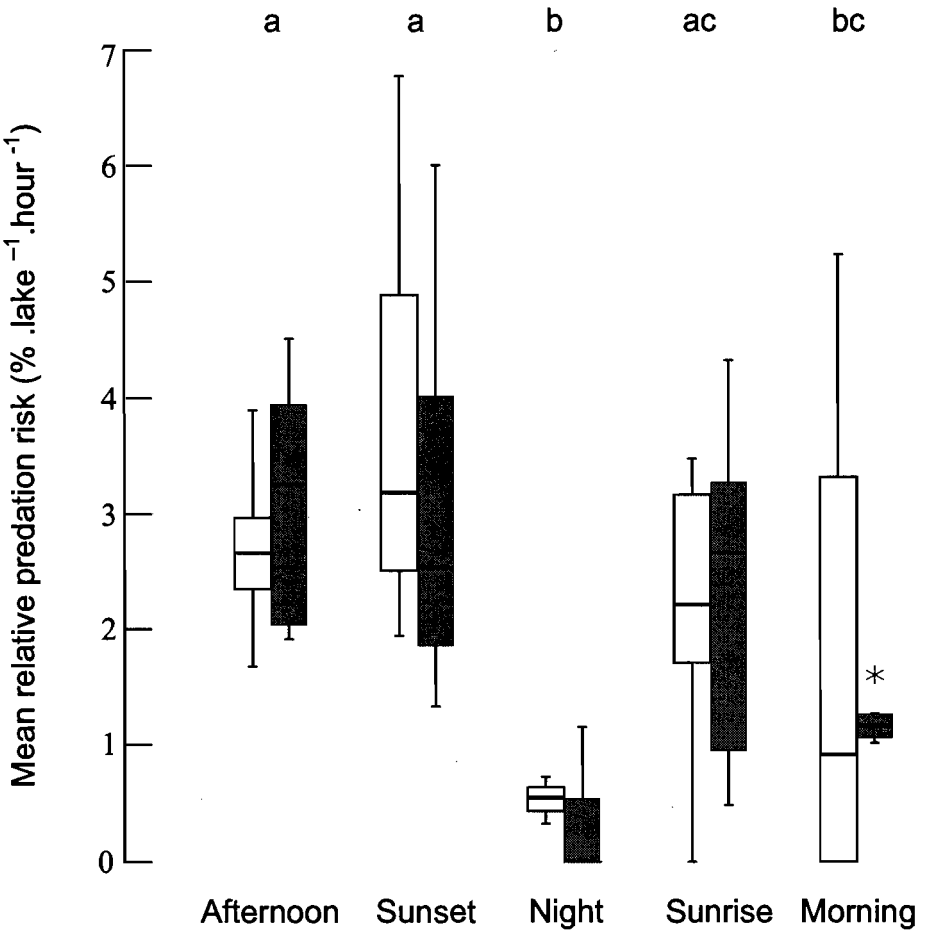
a
a
b
ac
bc
Mean relative predation risk (% .lake $^{-1}$.hour $^{-1}$)
0
1
2
3
4
5
6
7
*
Afternoon
Sunset
Night
Sunrise
Morning

Figure 3

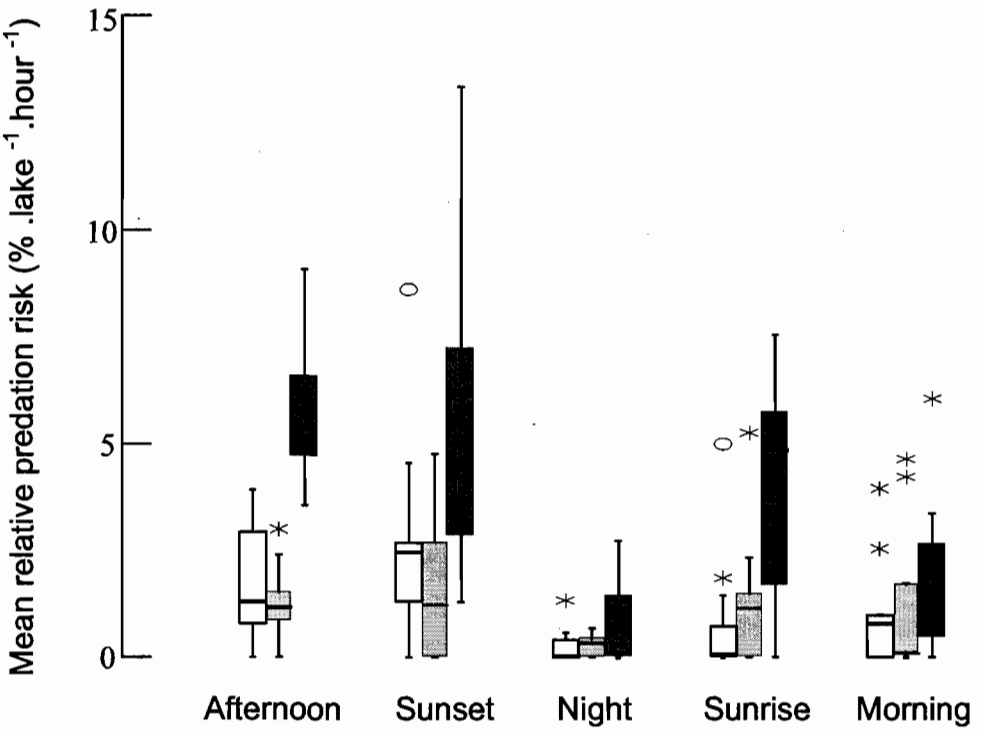
Mean relative predation risk (% .lake -1.hour -1)
15
10
5
0
Afternoon
Sunset
Night
Sunrise
Morning

Figure 4

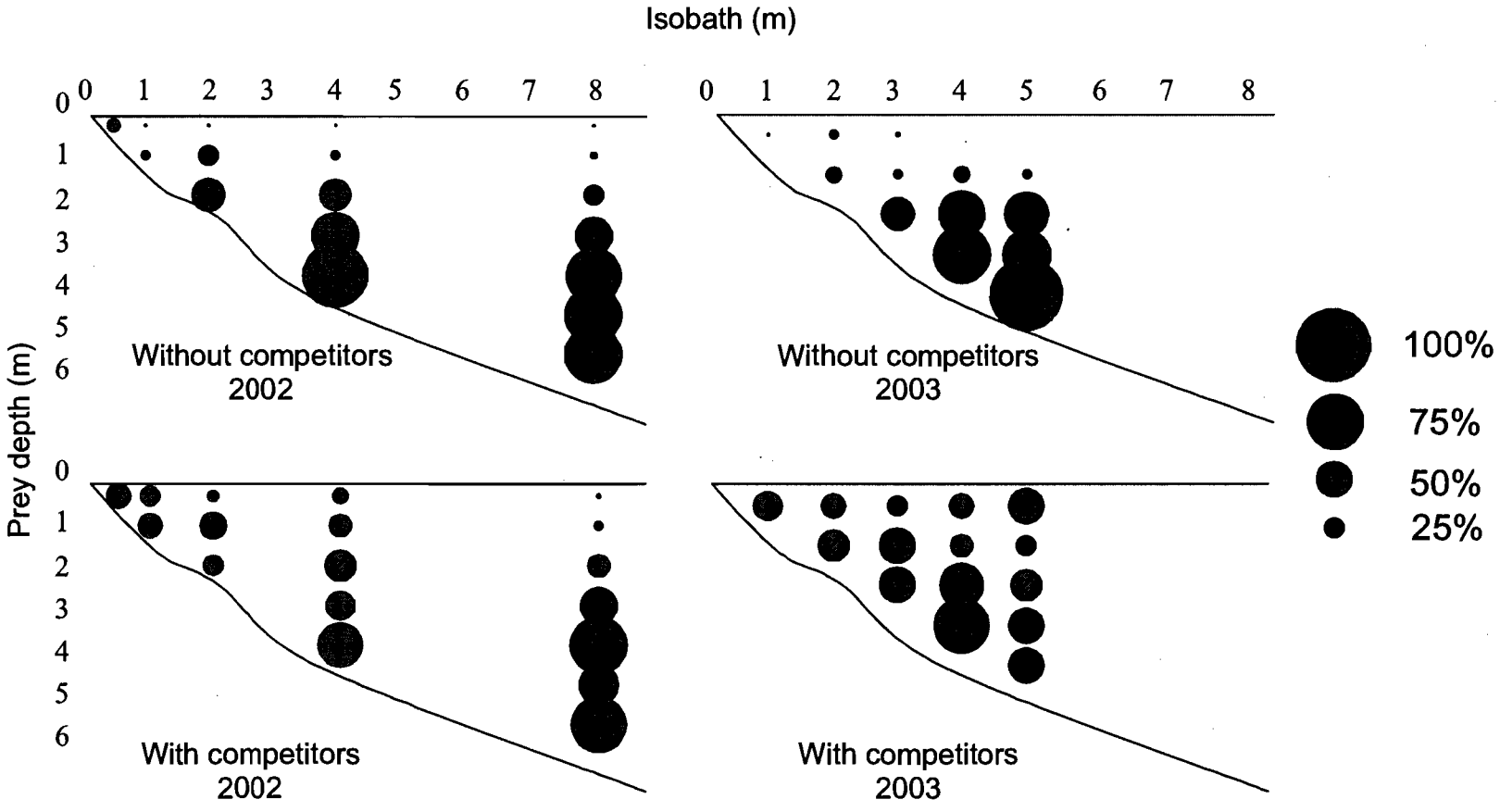
Isobath (m)
0 1 2 3 4 5 6 7 8
Prey depth (m)
0 1 2 3 4 5 6
Without competitors
2002
Without competitors
2003
With competitors
2002
With competitors
2003
100%
75%
50%
25%

Figure 5

CHAPITRE III

DOES PREDATION RISK INFLUENCE MACRO- AND MICROHABITAT USE BY NORTHERN REDBELLY DACE?[1]

Angélique Dupuch, Pierre Magnan, Andrea Bertolo, Lawrence M. Dill and Marcel Proulx

Angélique Dupuch, Pierre Magnan[2], Andrea Bertolo, Marcel Proulx. Groupe de Recherche sur les Ecosystèmes Aquatiques, Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières (Québec), G9A 5H7, Canada

Lawrence M. Dill. Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby (British Columbia), V5A 1S6, Canada

[1] Dupuch, A., Magnan, P., Bertolo, A., Dill, L. M. and Proulx, M. This article has been submitted for publication.

[2] Corresponding author (e.mail: pierre.magnan@uqtr.ca; tel.: 001 819 376 5011 # 3375; fax: 001 819 376-5084)

Résumé

Le ventre rouge du nord, *Phoxinus eos*, effectue des migrations nycthémérales entre les zones pélagique et littorale des lacs du bouclier canadien. Il vit en bancs et utilise préférentiellement les habitats structurés de la zone littorale durant la journée, se disperse dans la zone pélagique au coucher du soleil pour s'alimenter sur le zooplancton, et retourne dans la zone littorale au lever du soleil. Nous prédisons que (i) à l'échelle du lac, l'abondance de ventres rouges du nord dans la zone littorale durant la journée est positivement corrélée au risque de prédation dans la zone pélagique et (ii) à l'échelle de la zone littorale, l'abondance de ventres rouges du nord dans les habitats structurés est positivement corrélée au risque de prédation dans cette zone. Ces prédictions ont été testées au moyen de trappes à mennés placées dans des habitats structurés et des habitats sans structure dans la zone littorale de 13 lacs du bouclier canadien, et en utilisant les estimations du risque relatif de prédation du ventre rouge du nord dans les zones pélagiques et littorales obtenues à partir d'expériences d'attachement. Nous avons trouvé que (i) l'abondance moyenne des ventres rouges du nord dans la zone littorale était positivement corrélée au risque relatif de prédation dans la zone pélagique, (ii) les individus préféraient les habitats structurés aux habitats sans structure dans la zone littorale, (iii) cette préférence n'était pas reliée au risque relatif de prédation en zone littorale, mais diminuait quand le risque relatif de prédation augmentait dans la zone pélagique. A l'échelle du lac, nos résultats supportent l'hypothèse que le ventre rouge du nord entre dans la zone littorale pour éviter les prédateurs pélagiques. A l'échelle de la zone littorale, la flexibilité des tactiques anti-prédateurs du ventre rouge du nord pourrait expliquer la distribution spatiale des individus entre les habitats structurés et les habitats sans structure.

Abstract

Northern redbelly dace, *Phoxinus eos*, exhibit diel onshore–offshore migrations in Canadian Shield lakes. They form shoals and preferentially use structured habitats in the littoral zone during the day, disperse in the pelagic zone at sunset to feed on zooplankton, and then return to the littoral zone at sunrise. We predicted that (i) at the lake level, the abundance of dace in the littoral zone during the day would be positively correlated with predation risk in the pelagic zone, and (ii) at the littoral zone level, the abundance of dace in structured habitats would be positively correlated with predation risk in this zone. These predictions were tested by means of minnow traps placed in both structured and open water habitats in the littoral zone of 13 Canadian Shield lakes and using estimates of the relative predation risk of dace in both the pelagic and the littoral zones obtained from tethering experiments. We found that (i) the mean abundance of dace in the littoral zone was postively correlated with the relative predation risk in the pelagic zone, (ii) dace preferentially used structured over open water habitats in the littoral zone, and (iii) this preference was not related to relative predation risk in the littoral zone, but decreased as the relative predation risk increased in the pelagic zone. At the lake level, our results support the hypothesis that dace enter the littoral zone to avoid pelagic piscivores. At the littoral zone level, the flexibility in antipredator tactics could explain the spatial distribution of dace between structured and open water habitats.

Introduction

Many studies have shown that prey fish adapt their habitat selection in order to reduce predation risk (Lima & Dill, 1990; Lima, 1998). Habitats differ in both biotic and abiotic characteristics (including predation risk), and spatial heterogeneity occurs at different scales. Kramer *et al.* (1997) suggested that habitat selection by fish is a hierarchical process in which a general area is first selected (e.g., a lake or stream) followed by the selection of a macrohabitat (e.g., nearshore, riffle, pool) and finally by progressively smaller-scale decisions regarding local habitat characteristics (microhabitat; e.g., depth or structural complexity). This concept has been examined in birds and mammals (e.g., Orians & Wittenberger, 1991; Schaefer & Messier, 1995; Rolstad & Loken, 2000) but rarely in aquatic organisms (but see Bult *et al.*, 1998; Crook *et al.*, 2001). Yet, given that the spatial distribution of fish is associated with a set of habitat characteristics that depends on spatial scale (Poizat & Pont, 1996; Bult *et al.*, 1998; Crook *et al.*, 2001; Brind'Amour *et al.*, 2005), it could be expected that habitat selection results from such a hierarchical decision-making process. Many studies have shown that prey fish avoid predator-rich or refuge-poor habitats at the macroscale to decrease predation risk (e.g., pelagic zone of lakes; Lima, 1998). At the microscale, prey fish increase the use of structurally complex habitats (such as submerged vegetation and woody structures) when predation risk is high (Lima & Dill, 1990; Lima, 1998).

Refuge habitat use is often associated with lost foraging opportunities and increased resource competition (Werner *et al.*, 1983; Sih, 1997). Consequently, it could be expected that threatened fish adapt their habitat use to the level of predation risk (Helfman, 1989; Krause *et al.*, 1998, 2000) in an attempt to maximize their fitness (Lima & Dill, 1990; Lima, 1998). The use of refuge was also found to be related to prey size (Krause *et al.*, 1998; Dowling & Godin, 2002; Mirza & Chivers, 2003). Since the vulnerability of prey decreases as their body size increases (Sogard,

1997), prey fish of different sizes respond differently to the same level of predation risk (Krause *et al.* 1998, 2000; Dowling & Godin, 2002).

Northern redbelly dace, *Phoxinus eos*, exhibit diel onshore–offshore migrations in Canadian Shield lakes (Naud & Magnan, 1988; Gauthier *et al.*, 1997). They form shoals in the littoral zone during the day, disperse in the pelagic zone at sunset to feed on zooplankton, and then return to the littoral zone at sunrise. There is variability around this general pattern, with a small number of dace being observed outside the littoral zone during daytime (Naud & Magnan, 1988; Comeau & Boisclair, 1998; Gaudreau & Boisclair, 1998). Naud & Magnan (1988) suggested that northern redbelly dace use the littoral zone during daytime to reduce their predation risk by brook trout, *Salvelinus fontinalis*, a visual predator (Power, 1980). In agreement with this hypothesis, tethering experiments have shown that the relative predation risk of dace was significantly higher during daytime than during the night (Dupuch *et al.*, submitted). Also, Gaudreau & Boisclair (1998) showed that the presence of pelagic piscivores such as brook trout significantly reduced the number of dace present outside the littoral zone. Furthermore, dace preferentially use structured habitats that include vegetation and woody structures in the littoral zone of lakes (Naud & Magnan, 1988; He & Lodge, 1990; MacRae & Jackson, 2001; Jacobus & Ivan, 2005). As many studies have shown that fish density in the littoral zone is generally higher in more structurally complex habitats (e.g., Lewin *et al.*, 2004), the results described above suggest that predation risk is the causal mechanism of this pattern. However, this has seldom been the subject of a specific test in the field due to the difficulties of estimating predation risk in nature (but see Rozas & Odum, 1988). In the laboratory, the use of structured habitats allowed dace to significantly reduce the number of attacks and captures by brook trout (East & Magnan, 1991), supporting the predation risk hypothesis. Furthermore, dace are able to adapt the intensity of their antipredator response with the level of predation risk (Dupuch *et al.*, 2004). Thus, this system is a good model to test the effect of predation risk level on habitat use of prey fish at both the macro- and microscale.

Previous studies showed that brook trout prey upon dace (East & Magnan, 1991; Lacasse & Magnan, 1992). Furthermore, the occurrence of dace in the diet of brook trout was higher in lakes containing white sucker, *Catostomus commersonii*, and/or creek chub, *Semotilus atromaculatus*, than in lakes containing only brook trout (East & Magnan, 1991; Tremblay & Magnan, 1991; Lacasse & Magnan, 1992), suggesting that the predation risk of dace is higher in lakes containing white sucker and/or creek chub than in lakes containing only brook trout (hereafter referred to as lakes "with competitors" and "without competitors," respectively).

The goal of this study was to test whether habitat selection by northern redbelly dace is a hierarchical process associated with spatial scale (from macro- to microhabitat). In this context, if dace use the littoral zone to avoid pelagic piscivores, we predicted that (i) their abundance in the littoral zone will be positively related with predation risk in the pelagic zone at the lake level, and (ii) their abundance in structured habitats (compared to open water habitats) will be positively related to the predation risk at the littoral zone level. We also tested whether the body length of dace influenced their habitat use in the littoral zone. We estimated the abundance of dace in both structured and open water habitats of the littoral zone as well as their predation risk in the littoral and pelagic zones of lakes with and without competitors.

Materials and methods

Study sites

The study was carried out in 13 lakes of the Mastigouche Reserve (Québec, Canada; 46°40′ N, 73°20′ W) from June to September 1989 and from July to August 2003. These lakes are oligotrophic and typical of the Canadian Shield but differ in their fish assemblages. We chose lakes with similar morphology and characteristics of structured habitats in the littoral zone; therefore, we assumed that dace density was relatively similar among lakes. The main characteristics and fish assemblages of the

study lakes are shown in Table 1. We considered that, besides brook trout, potential piscivores (fish and birds) were negligible in the study lakes. Creek chub is a generalist feeder (Scott & Crossman, 1974), with large individuals (total length > 135 mm) feeding on small fish (e.g., Gilliam & Fraser, 1987). Given the low abundance of large creek chub in the study lakes (A. Dupuch, personal observation), and the absence of small fish in stomach contents of individuals captured in lakes similar to our study (Magnan & Fitzgerald, 1982, 1984), we assumed that this species was a negligible predator for dace. Furthermore, piscivorous birds (common loon, kingfisher and great heron) were rarely observed on the study lakes. So, like for creek chub, we considered their effect on the relative predation risk of northern redbelly dace as negligible compared to brook trout.

Experimental set-up

In 1989, eight lakes were sampled three times between June and September. In 2003, seven lakes were sampled three times over one week in July or August. To estimate dace abundance, we used baited minnow traps (with constant quantities of bread) set in the shallow littoral zone (water depth < 1 m) from 18h00 to 8h00 in 1989 and from 11h00 to 13h00 in 2003. The 1989 and 2003 experiments were part of projects having different logistical constraints, explaining the different fishing periods. However, both covered daylight periods. Traps were placed in two types of habitat (15 and 10 traps in each habitat type in 1989 and 2003, respectively): a structured habitat, characterized by either numerous rigid and tangled stems of *Cassandra calyculata* and *Sparganium* sp. or immersed wood (trees or branches), and an open water habitat without any structures. For both years, dace captured in each trap were counted. In 2003, 20 randomly sampled individuals per trap were sacrificed with an overdose of MS-222 and preserved in 95% alcohol for further laboratory analyses (total length for the present study).

Predation risk was estimated in the study lakes in 2003 with chronographic tethers (Danilowicz & Sale, 1999; Dupuch *et al.*, submitted). Briefly, 30 tethered dace

were set in each lake at different combinations of depth x water column isobath (isobaths = 1, 2, 3, 4 and 5 m; depths = 0.5, 1.5, 2.5, 3.5 and 4.5 m). During daytime, dace were rarely observed outside the areas used for tethering in lakes containing brook trout (Naud & Magnan, 1988; Gaudreau & Boisclair, 1998). We estimated the predation risk in both the littoral and pelagic zones based on dace tethered at the ≤ 2 m and > 2 m isobaths, respectively (submerged vegetation was rare beyond the 2 m isobath). Tethered dace were placed in open areas in the littoral zone (i.e., without vegetation or wood) to avoid entanglement. The predation risk was estimated as the proportion of missing dace after a given period of time (here 17 hours; see Chapter II for details). The mean predation risks in the littoral and pelagic zones of each lake are given in Table 1.

Statistical analyses

We analyzed the 1989 and 2003 data separately in order to validate the results of 2003 with those of 1989. For each sampling year, we used a mixed model approach (MIXED procedure of SAS 9.1.3; 2002 SAS package) with repeated measures and nested designs (lake was nested into the fish assemblage) to model dace CPUE (mean number of dace.trap^{-1}.habitat^{-1}.day^{-1}). The effects of habitat type (0 = open water habitat; 1 = structured habitat), fish assemblage (0 = without competitors; 1 = with competitors) and their interaction were tested for both sampling years. In addition to these variables, we also tested the effects of both littoral and pelagic predation risk and their interactions with habitat type (i.e., [littoral predation risk x habitat type] and [pelagic predation risk x habitat type]) on the CPUE of 2003. Given that a preliminary analysis showed that (i) the average predation risk of dace was not significantly higher in lakes with competitors than without (Dupuch *et al.*, submitted), and that (ii) fish assemblage and the predation risks in the littoral and pelagic zones were not collinear, we tested all these variables in the same analysis. Consequently, we interpreted the variable "fish assemblage" as an effect of fish species composition independent of predation risk.

For the analysis performed on the 1989 data, the sampling period (1 = beginning of summer; 2 = middle of summer; 3 = end of summer) was introduced into the model only to control for its effect on CPUE and so was not used in the interactions with the other variables. For 2003, the Akaïke Information Criterion (AIC; Burnham & Anderson, 2002) showed that a model without repeated measures better explained the CPUE. Thus, we present the mixed model that includes only the nested design. Removing the repeated-measure design from the model did not qualitatively change the results. CPUE were log (x + 1) transformed to normalize the residuals and reduce their heteroscedasticity.

Results

The analysis performed on the 1989 data showed that the average dace abundance in the littoral zone was significantly higher (i) in lakes with competitors than without, and (ii) in structured than in open water habitats (Table 2). Moreover, dace abundance in structured habitats was significantly higher in lakes with competitors than without (the [fish assemblage x habitat type] term was significant; Table 2), leading to a higher proportion of dace in structured habitats in lakes with competitors than without (Fig. 1).

The analysis of the 2003 data gave qualitatively the same results (Table 2; Fig. 1). Furthermore, this analysis showed that, on average, the dace abundance in the littoral zone was significantly and positively correlated with the pelagic predation risk and negatively correlated with the littoral predation risk. However, the increase of dace abundance in the littoral zone with the increase in pelagic predation risk was higher in open than in structured habitats (the [pelagic predation risk x habitat type] term was significant; Table 2). This led to a negative correlation between the proportion of dace captured in structured habitats and the pelagic predation risk (Fig. 2). Moreover, the effect of the littoral predation risk was not significantly different

between habitat types (the [littoral predation risk x habitat type] term was not significant; Table 2).

The mean size ± S.D. and the size range of dace captured in traps was 54.3 ± 6.8 mm and 40.1–76.7 mm, respectively. We did not observe differences in the mean lengths of dace between structured and open water habitats (Kolmogorov-Smirnov test, $p > 0.05$ in all lakes).

Discussion

Habitat selection by northern redbelly dace was related to both structural complexity and predation risk. The fact that the average abundance of dace in the littoral zone (depth < 1 m) was significantly and positively correlated with the pelagic predation risk supports the hypothesis that at the lake level, dace enter the littoral zone to reduce their predation risk by pelagic piscivores. The proximity of structured habitats and the rare presence of brook trout in the warm waters (Bourke *et al.*, 1996) make the littoral zone a safer habitat for dace than deeper areas.

At the littoral zone level, dace were on average more numerous in structured than in open water habitats, a distribution pattern that has been observed in other studies (see references in the Introduction). This preference for structured habitats compared to the open water habitat was not related to dace size, but the size range of dace captured in minnow traps was small.

Contrary to our expectations, the abundance of dace in structured habitats (compared to the open water habitat) was not positively correlated to the predation risk in the littoral zone. This does not contradict the often-accepted explanation that dace use these habitats to reduce their predation risk (e.g., Naud & Magnan, 1988). Although the use of structured habitats to avoid predation is common in aquatic species (Lima & Dill, 1990; Lima, 1998), prey fish do not systematically shift to structured habitats in the presence of predators (e.g., Jacobsen & Berg, 1998; Pink *et*

al., 2007). Different, though not mutually exclusive, hypotheses could explain this unexpected result. First, the availability of structured habitats limits prey abundance in these habitats (Rangeley & Kramer, 1998). Given that submerged vegetation and woody debris were abundant in the littoral zones of the study lakes (A. Dupuch, pers. observ.), we have no reason to raise this hypothesis for our system. Second, shallow habitats in the littoral zone are also refuge habitats for prey fish (Lima, 1998). He (1986) observed that dace aggregate in the very shallow water in the littoral zone in the presence of predators. The use of an alternative refuge habitat by dace could thus explain the absence of a positive correlation between dace abundance in structured habitats and relative predation risk. Furthermore, sheltering is often associated with a reduction of the prey's activity level (Lima, 1998), which could explain the reduced dace CPUE as the littoral predation risk increased. Third, dace shoal when in the littoral zone, and a preference for shoaling over refuge use in response to predation risk could also explain our results. Such a preference for shoaling over sheltering behaviour has been observed in northern redbelly dace (Pink *et al.*, 2007). These authors showed that after the introduction of brook trout in lakes, dace did not increase their use of structured habitats but significantly increased shoal size. Ashley *et al.* (1993) also showed that northern redbelly dace accept the risk imposed by a nearby predator when their shoal size was greater than 10 individuals: the larger the group size, the greater the benefits from the dilution and confusion effects (Pitcher, 1986; Godin, 1997; Krause & Ruxton, 2002). Shoaling behaviour also has the advantage of allowing individuals to search for food by switching among habitats while reducing predation risk (Pitcher & Parrish, 1993; Eklov & Persson, 1995; Godin, 1997), whereas sheltering is often associated with lost foraging opportunities and increased resource competition within the refuge habitat (Werner *et al.*, 1983; Sih, 1997).

Layman & Smith (2001) showed that *Fundulus heteroclitus* are attracted to minnow traps due to structure, perhaps as a behavioural adaptation to minimize predation risk. Furthermore, Robichaud *et al.* (2000) suggested that a trap in open

water habitats is more attractive than in structured habitats. Consequently, it could be expected that dace used minnow traps as refuges, particularly in open water habitats, and that their attraction to traps increased with predation risk. Thus, our sampling technique could also explain the higher CPUE in open water than in structured habitats as the pelagic predation risk increases, a counterintuitive result if dace use structured habitats as refuges. However, laboratory experiments showed that dace were attracted to traps, but that this attraction decreased as predation risk increased (A. Dupuch, unpub. data). In fact, we observed during this experiment that dace increased their shoaling behaviour when predation risk was high rather than searching for a structure (i.e., the trap) to hide (A. Dupuch, pers. observ.). Shoaling behaviour thus appears to be an important antipredator strategy in dace. All these results combined suggest that dace use several different antipredator tactics, leading to an unexpected spatial distribution of dace in the littoral zone of lakes.

For both years, the fish assemblage significantly influenced the spatial distribution of dace. Dace abundance in the littoral zone was higher in lakes with competitors than without, especially in structured habitats. Based on previous studies, we considered the presence of competitors in lakes as a factor that indirectly increased predation risk of dace. However, given (i) that the predation risk was similar in both the fish assemblages (Dupuch *et al.*, submitted), (ii) that the fish assemblage effect was estimated after controlling for the effects of the littoral and pelagic predation risk, and (iii) that creek chub, white sucker and pearl dace shared the littoral zone with northern redbelly dace, the higher abundance of northern redbelly dace in structured habitats in lakes with competitors than without could be a response to interspecific interactions rather than to predation risk. Interspecific interactions have been shown to directly affect the use of structured habitats by fish (e.g., Werner & Hall, 1977; Schofield, 2003). In the presence of competitors, the use of structured habitats by dace likely results from a combination of both interspecific competition and predation risk.

Acknowledgments

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Table 1: Lake area, mean depth, study year, fish species composition and mean predation risk in the littoral and pelagic zones of the study lakes. Sf: *Salvelinus fontinalis*; Pe: *Phoxinus eos*; Cc: *Catostomus commersonii*; Sa: *Semotilus atromaculatus*; Sm: *Semotilus margarita.* n.d.: not determined.

Lake name	Area (ha)	Mean depth (m)	Study year		Fish assemblage					Mean predation risk ± SD (%)	
			1989	2003	Sf	Pe	Cc	Sa	Sm	Littoral zone	Pelagic zone
Without competitors											
Bondi	25.7	8.1		√	√	√				0 ± 0	38 ± 5
Charme	22.0	3.2	√		√	√					
Cerné	13.2	4.4		√	√	√				23 ± 9	42 ± 20
Diablos	9.1	3.5	√		√	√					
Lafond	46.7	7.9		√	√	√				6 ± 10	20 ± 2
Osborn	10.8	4.8	√	√	√	√				7 ± 12	40 ± 10
Vautour	7.2	4.8	√		√	√					
With competitors											
Gauthier	36.9	n.d.		√	√	√		√	√	20 ± 28	15 ± 15
Grignon	29.6	7.9	√	√	√	√	√	√		18 ± 17	62 ± 20
Grosse	8.0	6.2		√	√	√	√	√		75 ± 25	48 ± 35
Joe	23.3	n.d.	√		√	√	√				
Sauterelle	8.1	5.4	√		√	√	√		√		
Vert	17.1	8.7	√		√	√	√	√			

Table 2: Results of the mixed models performed on the 1989 and 2003 data to predict dace CPUE in structured and open water habitats in the littoral zone of study lakes.

Variables	Estimates	S.E.	df	F-value	P-value
1989					
Intercept	+ 2.20	0.30			
Time 1	+ 1.56	0.30	2/35.3	26.03	< 0.001
Time 2	- 0.37	0.30			
Time 3	0.00				
Habitat type	- 1.08	0.33	1/34.5	6.52	0.015
Fish assemblage	- 0.70	0.35	1/6.31	21.56	0.003
Habitat type x fish ass.	+ 0.95	0.47	1/24.5	4.04	0.052
2003					
Intercept	+ 1.67	0.45			
Habitat type	- 0.56	0.19	1/27.9	5.87	0.022
Fish assemblage	- 1.37	0.55	1/5.18	9.43	0.026
Habitat type x fish ass.	+ 0.55	0.24	1/27.9	4.98	0.034
Littoral predation risk	- 0.30	0.13	1/32.9	4.75	0.036
Pelagic predation risk	+ 0.56	0.11	1/31.8	5.98	0.020
Pel. pred. risk x fish ass.	+ 0.67	0.12	1/27.9	30.68	< 0.001
Litt. pred. risk x fish ass.					NS

Figure captions

Figure 1: Mean (± S.E.) proportion of dace captured in structured habitats of the littoral zone of lakes according to fish assemblage (white bars = without competitors; black bars = with competitors) for 1989 and 2003.

Figure 2: Variations in the proportion of dace captured in structured habitats of the littoral zone of lakes according to the predation risk in the pelagic zone (2003 data).

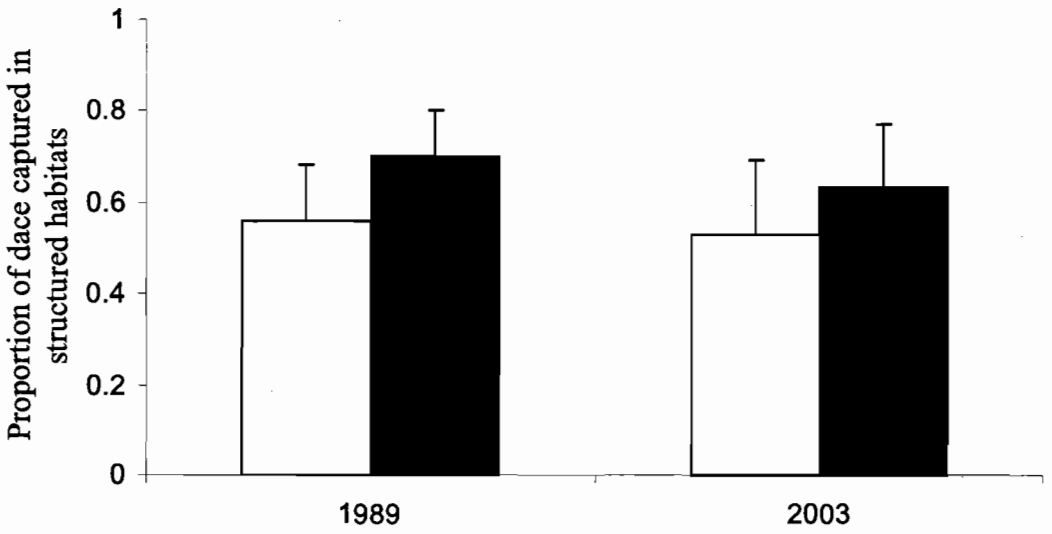
Proportion of dace captured in structured habitats
1
0.8
0.6
0.4
0.2
0
1989
2003

Figure 1

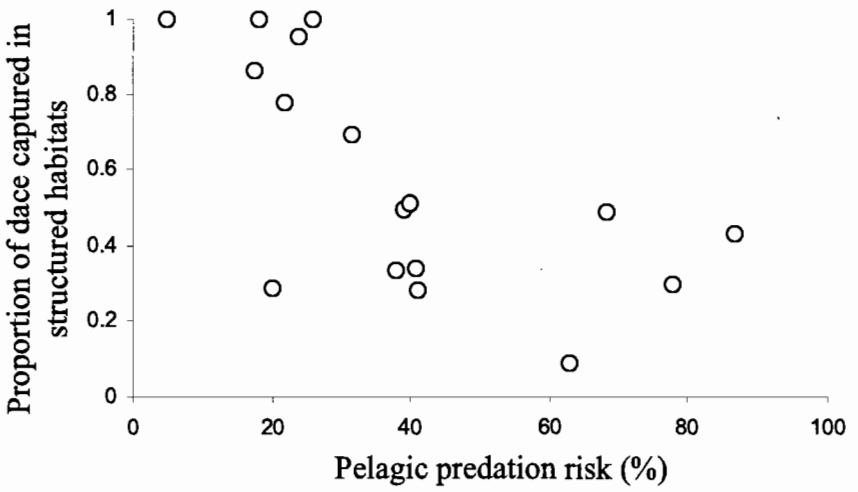
Proportion of dace captured in structured habitats
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
Pelagic predation risk (%)

Figure 2

CHAPITRE IV

TESTING THE EFFECTS OF RESOURCE DISTRIBUTION AND INHERENT HABITAT RISKINESS ON SIMULTANEOUS HABITAT SELECTION BY PREDATORS AND PREY[1]

Angélique Dupuch, Lawrence M. Dill and Pierre Magnan

Angélique Dupuch, Pierre Magnan[2]. Groupe de Recherche sur les Ecosystèmes Aquatiques, Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières (Québec), G9A 5H7, Canada

Lawrence M. Dill. Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby (British Columbia), V5A 1S6, Canada

[1] Dupuch, A., Dill, L. M., and Magnan, P. This article has been submitted for publication.

[2] Corresponding author (e.mail: pierre.magnan@uqtr.ca; tel.: 001 819 376 5011 # 3375; fax: 001 819 376-5084)

Résumé

Des études théoriques ont utilisé le modèle de la Distribution Idéale et Libre pour étudier des systèmes prédateur-proie à trois niveaux trophiques où les prédateurs et les proies peuvent se déplacer librement. Une prédiction commune à ces modèles est que la distribution des proies ne devrait pas (ou presque pas) être influencée par la distribution de la ressource alimentaire. De plus, si le risque inhérent à l'habitat varie, les modèles prédisent que la distribution des proies devrait être principalement influencée par le risque inhérent à l'habitat, les proies évitant les habitats les plus risqués, quelle que soit la distribution de la ressource alimentaire. Afin de tester cette prédiction, nous avons fait des expériences en laboratoire dans lesquelles les prédateurs (le mulet à cornes, *Semotilus atromaculatus*) et les proies (le ventre rouge du nord, *Phoxinus eos*) étaient libres de se déplacer entre deux parcelles qui différaient en terme de quantité de ressources alimentaires et de risque inhérent à l'habitat. Quand ils étaient seuls, (i) les mulets et les ventres rouges du nord préféraient la parcelle la plus riche en ressources alimentaires et (ii) la distribution spatiale des ventres rouges du nord était inversement reliée au risque inhérent à l'habitat. En présence de mulets contraints de rester dans les parcelles d'alimentation, la distribution spatiale des ventres rouges du nord était inversement reliée à celle des mulets. Quand les parcelles différaient en terme de quantité de ressources alimentaires et de risque inhérent à l'habitat, la distribution spatiale des ventres rouges du nord était principalement influençée par la distribution de la ressource alimentaire, et peu par le risque inhérent à l'habitat en absence de prédateurs. En présence de mulets, les ventres rouges du nord ont significativement diminué l'utilisation de la parcelle la plus risquée comparé aux expériences sans prédateurs. Cependant, contrairement à la prédiction des modèles, la distribution de la ressource alimentaire influençait encore de manière significative la distribution spatiale des ventres rouges du nord quand les prédateurs étaient présents. Finalement, les ventres rouges du nord s'agrégeaient de plus en plus dans une troisième parcelle, totalement

sécuritaire mais n'offrant aucune ressource alimentaire, au fur et à mesure que le nombre de mulets présents dans les deux parcelles d'alimentation augmentait. Ainsi, l'influence de la distribution de la ressource alimentaire et du risque inhérent à l'habitat sur la distribution spatiale des proies semble varier avec l'intensité du risque de prédation, et l'évitement des prédateurs semble déterminer le choix de l'habitat par les proies quand le risque de prédation est élevé.

Abstract

Theoretical models have extended the Ideal Free Distribution model to examine predator-prey systems having three trophic levels, when both predator and prey are allowed to move freely. One consistent prediction made by such models is that the spatial distribution of prey should not be (or nearly so) influenced by resource distribution. Furthermore, if inherent habitat riskiness varies, models predict that prey distribution should be mainly determined by the inherent habitat riskiness (e.g., structural complexity or light level), with prey avoiding the inherently riskier habitats regardless of resource distribution. In order to test this prediction, we conducted laboratory experiments in which both predators (creek chub, *Semotilus atromaculatus*) and prey (northern redbelly dace, *Phoxinus eos*) were free to move between feeding patches differing in resource quantity and habitat riskiness. When alone, (i) creek chub and northern redbelly dace both preferred the more food-rich patch, and (ii) the spatial distribution of dace was inversely related to the inherent habitat riskiness. In the presence of chub fenced into feeding patches, the spatial distribution of dace was inversely related to that of creek chub. When the patches differed in both riskiness and resource quantity, the spatial distribution of dace was mainly influenced by resource distribution in the absence of predators. In the presence of creek chub, the dace significantly decreased their use of the inherently riskier patch compared to when predators were absent. However, contrary to the models' prediction, food distribution still significantly influenced dace distribution when predators were present. Finally, dace aggregated increasingly in a third, totally safe area (but one offering no food) as the number of chub present in both feeding patches increased. Thus, the influence of resource distribution and inherent habitat riskiness on prey distribution seems to vary with the level of predation risk, and predator avoidance seems to determine prey habitat choice when predation risk is high.

Introduction

Understanding the responses of predators and prey to each other is a central topic in behavioural ecology, a key issue being their use of habitats (Sih 2005). Many studies have explored habitat use by prey and predators, and there is ample evidence that prey prefer the low-predator habitats and predators the prey-rich habitats (Lima and Dill 1990; Lima 1998; Sih 2005). However, these studies mostly focused on the behaviour of prey or predators when the distribution of the other species is fixed in space (e.g., using caged predators, chemical cues, or immobile prey). Lima (2002) highlighted the scarcity of both theoretical and empirical knowledge of predator and prey space use when both are allowed to move freely. Intuitively, it could be expected that predators favour prey-rich habitats, which should cause a shift in prey habitat use, after which predators follow the prey, and so on. However, the consequences of this behavioural race on predator-prey spatial distribution are not obvious, i.e., whether an equilibrium distribution would result, and what it would be.

Game theory (Maynard Smith 1982) has provided a conceptual framework for theoretical studies investigating this issue (e.g., Iwasa 1982; Van Baalen and Sabelis 1993; Hugie and Dill 1994; Alonzo 2002; Abrams 2007). Typically, these theoretical studies have extended the Ideal Free Distribution (IFD; Fretwell and Lucas 1970; Kacelnik *et al.* 1992) model to examine three-level trophic systems, in which a predator species feeds on a prey species, which feeds on a resource fixed in space. Predator and prey can move freely among habitats that differ in their resource quantity and/or in their inherent habitat riskiness (a habitat feature that is independent of predator density, for example, one that might reflect cover, structural complexity or light level; Hugie and Dill 1994). On one hand, predators use habitats in a manner that maximizes their foraging success, which is a function of prey density, competition level and inherent habitat riskiness. On the other hand, prey use habitats to balance their risk of predation and the benefits of foraging (which is a function of resource quantity and competition level). These theoretical studies showed that

predator and prey spatial distributions can reach an evolutionary stable strategy (ESS), where no individual can improve its fitness by shifting habitat (e.g., Iwasa 1982; Van Baalen and Sabelis 1993; Hugie and Dill 1994; Alonzo 2002; but see Abrams 2007). Although the models differ in their details, one consistent prediction is that habitat use by prey should not be affected by resource distribution, or be only slightly affected, depending on the level of competition among prey and among predators (e.g., Hugie and Dill 1994; Sih 1998; Bouskila 2001; Alonzo 2002; Krivan and Schmit 2003; Luttbeg and Sih 2004). If habitats differ in both their resource quantity and inherent habitat riskiness, the spatial distribution of prey should be mainly determined by riskiness, with prey avoiding the inherently risky habitat, regardless (or nearly so) of resource distribution (Hugie and Dill 1994; Sih 1998; Luttbeg and Sih 2004). This prediction is quite different from results of theoretical and empirical studies that consider a fixed difference in predation risk between habitats. Indeed, these studies have shown that prey respond to both resource distribution and predation risk when choosing a feeding habitat (Gilliam and Fraser 1987; Abrahams and Dill 1989; Lima and Dill 1990; Grand and Dill 1997).

A few studies have focused on habitat selection by predators and prey when both can move freely (Sih 1984; Formanowicz and Bobka 1989; Bouskila 2001; Sih 2005; Hammond *et al.* 2007). These studies determined the effect of either resource distribution (Bouskila 2001; Sih 2005; Hammond *et al.* 2007) or inherent habitat riskiness (Sih 1984; Formanowicz and Bobka 1989; Bouskila 2001) on habitat selection by both prey and predators, but not of both factors simultaneously. The objective of our study was thus to test the prediction that the spatial distribution of prey should be mainly determined by riskiness, with prey avoiding the inherently riskier habitat, regardless (or nearly so) of resource distribution. In order to test this prediction, we conducted laboratory experiments in which both predators and prey were free to move between habitats differing in both inherent riskiness and resource quantity.

Materials and methods

The experiments were performed in a tank separated into two parts, each of which was 55 cm wide, 25 cm deep and 475 cm long (Fig. 1a), that we used as independent experimental units to perform two trials simultaneously. Water temperature was maintained at 14 ± 0.2°C and light intensity was kept low during trials (< 1.0 lux). A black curtain was placed around the tank to reduce the effects of external factors on fish behaviour. An automatic feeder was placed at each end of the experimental tanks to deliver different quantities of trout pellets (Fig. 1a). We considered the area around each feeder (55 cm x 45 cm) as an alternative feeding patch. Trout pellets not eaten by fish were collected in a plastic container on the bottom of the tank (Fig. 1b). A grid covered the container so that the fish did not have access to this uneaten food. Fish were filmed in each feeding patch from the top of the tank with four video cameras (Sony CCD-TR400; Fig. 1b) connected to a recording system.

The prey, northern redbelly dace (*Phoxinus eos*), and the predators, adult creek chub (*Semotilus atromaculatus*) used in the experiments were collected with baited minnow traps and fyke nets in Lac de la Grosse of the Mastigouche Reserve (Québec, Canada; 46°40′N, 73°20′W) in June 2006. This lake also contained brook trout (*Salvelinus fontinalis*) and white suckers (*Catostomus commersonii*), and dace were subject to both trout and creek chub predation (Dupuch *et al.* submitted). Approximately 1000 northern redbelly dace (mean total length ± S.D., 6.4 ± 0.5 cm) and 132 creek chub (17 ± 0.8 cm) were used in the experiments. Dace and chub were held in two and four holding tanks, respectively, at 14 ± 0.2°C under a 12h:12h light:dark regime. Fish were fed *ad libitum* once a day with commercial trout pellets (Corey Aquaculture 0.5 GR and 1.0 GR mixed for dace; Corey Aquaculture 1.5 GR for creek chub).

We conducted six sets of experiments to test:

(i) whether dace and creek chub distributed themselves between two patches according to their resource quantity, i.e., input matching, as predicted by the IFD model (experiments *a* and *b* respectively);
(ii) whether dace adapted their spatial distribution to that of the predator's (experiment *c*);
(iii) whether dace adapted their spatial distribution to the inherent habitat riskiness in the absence of predators (experiment *d*);
(iv) whether inherent habitat riskiness affected the match between dace distribution and resource distribution in the absence or presence of predators (experiments *e* and *f*, respectively). The experiment with no predators (experiment *e)* was used as a control for the experiment with predators (experiment *f*). We compared the results of experiments *e* and *f* to test the prediction that in the presence of predators, prey should avoid the inherently riskier patch regardless (or nearly so) of resource distribution.

For all trials, groups of 50 dace (experiments *a*, *c*, *d*, *e* and *f*) or 20 creek chub (experiment *b*) were randomly assigned to each of the two experimental tanks and introduced into their centre sections between 7h30 and 9h30. Trout pellets were delivered from the automatic feeders in each patch as soon as fish were introduced to the experimental tank, for a period of seven hours. Fish had been deprived of food for a period of 24 h before each trial. In each experiment, five replicates (six for experiment *a*) were performed for each treatment level (i.e., for each food ratio, creek chub ratio, inherent habitat riskiness ratio, or combination of food x inherent habitat riskiness ratio). Fish were returned to their holding tanks at the end of each experiment, but because we alternated the holding tank from which we sampled experimental fish, dace and creek chub could not be subjected to more than one trial per two or four days, respectively. The treatment level as well as the food-poor patch and the safer patch in each channel were randomly designated before each trial.

During pilot experiments, we observed that antipredator behaviours were elicited in dace only if contact was possible between dace and creek chub (e.g., in

contrast to when they were separated by transparent Plexiglas). When we placed both dace (n = 50) and creek chub (n = 7) together in the experimental tank, we observed that, on average, about seven or eight predation events occurred per trial. As that number of predations was too high, we added a plastic grid tunnel (12 x 12 x 375 cm long) between the two feeding patches on the bottom of each experimental tank (Fig. 1), allowing dace to pass through but not creek chub. Thus, dace could use this tunnel to swim from one patch to the other without being attacked by creek chub, reducing the number of predation events during trials (to about 2-3 per trial on average). A distance of 40 cm separated the end of the tunnel from each food source (Fig. 1). Thus, creek chub mainly attacked dace when they left the tunnel to reach the food.

Attacks on dace and predation events occurred during experiments *c* and *f*. The alarm substance released from dace during these predation events (Dupuch *et al.* 2004) could thus have biased their behaviour during trials of these experiments, and potentially during trials of experiments *d* and *e,* due to the (unknown) persistence of alarm substance in the experimental system. Ideally, we should have removed the water from the tank (4000 L) and cleaned it after every trial in which a predation event occurred. However, this was not possible due to the limited capacity of our water treatment system. In order to reduce this bias, we changed 75% of the water volume of the tank (about 3000 L) after performing the trials of experiment *c*, and we waited two days before performing experiment *d,* which did not involve predation. Furthermore, we alternated experiments *e* and *f* in groups of 10 to 20 trials. When a group of trials without predators followed one with predators, we changed half of the water volume of the tank (2000 L) and waited one day before performing the next pair of trials.

Experiments *a* and *b: IFD in dace and creek chub*

Differences in habitat profitability were produced by delivering different quantities of trout pellets in the two feeding patches of each experimental tank. A total of 1.4 g of pellets for dace and 2.8 g for creek chub was split between the two

patches in the following ratios (patch 1: patch 2): 1:6, 1:3, 1:1, 3:1, 6:1, and continuously input by the automatic feeders over a period of seven hours. We determined during pilot trials that fish were not satiated with these quantities of food.

Experiment *c*: *Effect of spatial distribution of creek chub on dace distribution*

In each feeding patch, the automatic feeders delivered 0.7 g of pellets over a period of seven hours. Creek chub were maintained in each patch by a vertical partition of plastic grid that allowed dace but not creek chub to pass through (Fig. 1a). We also placed a circular plastic grid partition around the feeders to allow dace to feed on pellets but not creek chub (Fig. 1a). A total of seven creek chub were distributed between the two feeding patches in the following ratios (patch 1: patch 2): 1:6, 2:5, 3:4, 4:3, 5:2 and 6:1.

Experiment *d*: *Effect of inherent habitat riskiness on the spatial distribution of dace in the absence of predators*

In each feeding patch, the automatic feeders delivered 0.7 g of pellets over a period of seven hours. We simulated variation in inherent habitat riskiness by varying the densities of straws (to imitate plant stems in lakes) at both ends of the experimental tank (straw densities used were 111/m^2, 222/m^2 and 333/m^2, which are comparable to stem densities in vegetated areas of lakes in the study system). Different combination of straws/m^2 (111:333, 111:222, 222:222, 222:111, 333:111) were used to create the following inherent habitat riskiness ratios (patch 1: patch 2): 1:3, 1:2, 1:1, 2:1 and 3:1.

Experiments *e* and *f*: *Effect of habitat riskiness on the IFD of dace in the absence and presence of predators, respectively*

In these experiments, we used the same habitat riskiness ratios as in experiment *d* and the food ratios 1:3 and 3:1. These food ratios were used because the results of experiment *a* showed that the spatial distribution of dace at these two food

ratios (i) did not differ from the predictions of the IFD model (the 95% confidence interval [CI] included the expected value from IFD; 1:3: CI = 0.17–0.32; 3:1: CI = 0.47–0.76), and (ii) were significantly different from each other (N_{trials} = 6, U = 0.0, p = 0.004). We also placed a circular plastic grid partition around the feeders to allow dace but not creek chub to feed on the pellets (Fig. 1a). The combination of different food and inherent habitat riskiness ratios resulted in ten different treatments. For the experiment with predators (i.e., experiment *f*), 7 creek chub were introduced in the central section of the experimental tank at the beginning of the fourth hour of a trial and were free to move from one feeding patch to the other. We introduced creek chub at the beginning of the fourth hour because the results of pilot experiments showed that dace responded to resource distribution from the third to the sixth hour of a trial. We mimicked creek chub introduction in dumping only water in the central section of the experimental tank at the beginning of the fourth hour of trials in the experiment without predators (i.e., experiment *e*). This ensures that results from the experiment with predators were due to the presence of creek chub and not to the disturbance created during creek chub introduction. We counted the number of dace at the end of each trial with predators to determine the number of predation events that occurred.

Estimation of fish distribution

Attacks on dace and predation events began as early as the first hour after the introduction of creek chub to the experimental tank (experiment *f*). In several trials, creek chub activity and attacks on dace strongly decreased during the third hour after their introduction (counting the three hours of dace acclimation before the introduction of chub, the attacks on dace strongly decreased during the sixth hour after the beginning of an experiment). Based on these observations, the fifth hour of a trial was considered as the most appropriate period to determine the effects of resource distribution and inherent habitat riskiness on the spatial distribution of dace in the presence of predators. In order to compare results among experiments (*a*, *c*, *d*, *e*

and *f*), we estimated the spatial distribution of dace during the fifth hour of trials in all experiments.

To describe the spatial distribution of dace in these experiments, we used the mean proportion of individuals observed in patch 1 (Figure 1). For each trial, we first counted the number of individuals in each feeding patch every 2 minutes for dace and every minute for creek chub during the fifth hour of trials. We then used the average number of individuals observed in each patch i (i.e., N_i) during these 60 minutes to estimate the mean proportion of individuals observed in patch 1 (i.e., $N_1/(N_1+N_2)$).

For each trial of experiment *f*, we also counted the number of dace in each patch every 2 minutes for a period of 30 minutes from 2.5 to 3 hours after the beginning of the trial (i.e., just before the introduction of creek chub) to estimate the mean proportion of individuals observed in patch 1. It was essential that dace responded to resource distribution before the introduction of creek chub in experiment *f*. To meet this condition, we compared the mean proportion of dace in patch 1 before the introduction of creek chub (experiment *f*) to the mean proportion observed during experiment *e* for the same combination of food proportion x inherent habitat riskiness. Trials for which the proportion of dace in patch 1 before the introduction of creek chub (experiment *f*) was significantly different (i.e., not within the 95% CI) from that seen in experiment *e* were not considered (12 of 50 trials; experiment *f*) and were replaced by successful trials. This ensured that (i) the spatial distribution of dace in experiment *f* was not different from that in experiment *e* before the introduction of creek chub, so (ii) any difference in the spatial distribution of dace between experiments *e* and *f* was due to the presence of predators.

We did not consider trials in any experiment in which dace exhibited abnormal behaviour, i.e., where the entire group of dace stayed motionless in one of the patches. Furthermore, when patches differed in both riskiness and resource quantity in the absence of predators (experiment *e*), we did not consider trials in which the spatial distribution of dace was more influenced by inherent habitat riskiness than by food (i.e., trials in which less than 50% of dace were in the richer

patch). This means that despite the absence of predators, a majority of the dace must have perceived a threat coming from uncontrolled factors outside of the tank (6 of 50 trials). Finally, we did not consider trials in which the group of creek chub were either motionless and/or did not attack dace (1 of 50 trials; experiment *f*). All the trials that were not considered were redone to maintain the same sample size.

Statistical analyses

For each experiment, we used a general linear model (GLM) to determine if the different treatment levels (independent variables) were significantly related to the proportion of dace or creek chub in patch 1 during the fifth hour of the trial (dependent variable). The independent variables were the proportion of food delivered in patch 1 (experiments *a* and *b*), the proportion of predators in patch 1 (experiment *c*), the inherent habitat risk ratio (experiment *d*), and the inherent habitat risk ratio in interaction with the proportion of food delivered in patch 1 without predators (experiment *e*) and with predators (experiment *f*). The interactions [Food proportion x predator] and [Habitat riskiness x predator] were also tested (experiments *e vs. f*; predators absent *vs.* present respectively) in order to examine model predictions. If, in the presence of predators, prey avoid the inherently riskier habitat regardless (or nearly so) of resource distribution, we expected that the effect of inherent habitat riskiness on dace distribution would increase and that of food proportion would decrease in the presence of creek chub (i.e., both the interactions [Habitat riskiness x predator] and [Food proportion x predator] would be significant).

We also tested whether the slope of the relationship between resource distribution and fish distribution was significantly different from 1.0 in experiments *a* and *b* to test whether the proportion of dace and creek chub in patch 1 conformed to the IFD. Similarly, we tested if the mean proportion of dace in patch 1 for each combination of food x inherent habitat riskiness ratio differed from the IFD expectation in experiment *e*. Here, we considered that the proportion of dace in patch

1 was significantly different from IFD when the expected proportions (25% or 75%) were not included in the 95% CI of the observed distribution.

Results

The spatial distributions of both northern redbelly dace and creek chub responded to the resource quantities in the alternate patches (Fig. 2). However, these relationships did not conform to the predicted IFD because their slopes were significantly lower than 1.0 (dace: $F_{1,28} = 23.31$, $p < 0.001$; creek chub: $F_{1,23} = 27.77$, $p < 0.001$). This deviation from IFD results from an underuse of patch 1 by dace when it was the richer patch and an overuse of patch 1 by creek chub when it was the poorer patch. The proportion of dace was also inversely related to that of creek chub in patch 1 (Fig. 3) and to the inherent habitat riskiness in patch 1 in the absence of predators (Fig. 4).

In the absence of predators, when patches differed in both riskiness and resource quantity (experiment *e*), the spatial distribution of dace was mainly influenced by resource distribution ($R^2_{partial} = 0.68$; Table 1; Fig. 5) and, to a lesser extent, by the inherent habitat riskiness ($R^2_{partial} = 0.02$; Table 1; Fig. 5). Furthermore, the fact that feeding patches differed in their inherent riskiness decreased the expected match between resource quantity and the spatial distribution of dace. Indeed, dace distributed themselves as expected from IFD only when the richer patch was also the inherently safer patch (Table 2). Otherwise, dace significantly underused the richer patch when it was also the inherently riskier one.

In the presence of predators, the proportion of dace significantly decreased in the inherently riskier patch compared to trials when predators were absent (Fig. 5; Habitat riskiness x predator was significant; Table 3). However, contrary to expectation, the presence of predators did not change the effect of food distribution on dace distribution. The proportion of dace was always higher in the richer patch

relative to the poorer one, even in the presence of predators (Fig. 5; Food proportion x predator was not significant; Table 3). Resource distribution and inherent habitat riskiness ratio explained 34% and 14% respectively of the variation in the proportion of dace in patch 1 in the presence of predators (Table 1).

The mean number of dace observed per minute in the two patches combined was significantly lower in experiments with than without creek chub ($F_{6,280} = 16.28$, $p < 0.001$; Fig. 6). In presence of creek chub, the mean number of dace observed per minute in the two patches combined was reduced by an average of 20%. Furthermore, when creek chub were free to move between patches (experiment *f*), the proportion of dace leaving the feeding patches after introduction of chub increased significantly with the mean number of chub observed per minute in the two patches combined, to a maximum of 75% (Fig. 7).

The number of predation events occurring during a trial varied from 0 to 6 (mean ± S.D. = 2.2 ± 1.6) and significantly increased with the mean number of chub observed per minute in the two patches combined ($N_{trials} = 47$, $r_{spearman} = 0.43$, $p = 0.002$), but significantly decreased with the mean number of dace observed there ($N_{trials} = 47$, $r_{spearman} = -0.39$, $p = 0.006$).

Creek chub distribution was not significantly affected by either resource distribution or inherent habitat riskiness (GLM, $N = 50$, $p > 0.05$).

Discussion

As predicted, both dace and creek chub preferred the richer patch when alone (experiments *a* and *b*), but resource matching was imperfect. Many studies have shown that consumers generally under match the resource distribution for various reasons (Kennedy and Gray 1993), such as travel cost between habitats, imperfect knowledge of resource distribution (Abrahams 1986), and competitive interference among consumers (Sutherland 1983). Aggressiveness among creek chub (A. Dupuch,

pers. observ.) could partly explain their imperfect resource matching. Furthermore, we found that dace preferred patch 2 and creek chub preferred patch 1, an inherent tank effect that we cannot explain. This resulted in an underuse of patch 1 by dace when it was the richer patch and an overuse by creek chub when it was the poorer patch.

Like many prey, dace avoided predator-rich (experiment *c*) and refuge-poor patches (experiments *d* and *e*) (Lima and Dill 1990; Kramer *et al.* 1997; Lima 1998). Generally, prey balance energetic gains and predation risk when choosing a feeding habitat (Lima and Dill 1990). When patches differed in both resource quantity and inherent habitat riskiness, and predators were absent, dace underused the richer patch (relative to IFD predictions) when it was also the inherently riskier patch. This suggests that dace use the habitat's structural complexity as a proxy of predation risk, and trade-off energetic gains and predation risk even in the absence of a real predation threat.

Contrary to the prediction of models, dace distribution was mainly determined by resource distribution and to a lesser extent by inherent habitat riskiness even in the presence of predators free to move (experiment *f*). Given that prey and predator distributions should affect each other, one explanation could be that creek chub distribution was not as predicted by the models. Usually, models predicting that prey distribution should not be affected (or only slightly) by resource distribution also predict that predators should prefer habitats containing the highest resource quantity, even one they don't eat (Hugie and Dill 1994; Sih 1998; Luttbeg and Sih 2004). However, in our experiment, creek chub distribution was relatively uniform. The presence of the grid around the automatic feeders prevented creek chub from feeding on trout pellets (i.e., the resource), and may have prevented them from assessing the resource quantity in each patch and responding accordingly. The fact that creek chub did not prefer the richer patch could thus explain why resource distribution significantly influenced dace distribution.

A second explanation could be that game models predicting that resource distribution would not affect prey distribution considered prey fitness as independent of an individual's state (such as energy reserves or individual experience). Yet, empirical data suggest that models incorporating individual state in the feeding–mortality trade-off better predict behavioural decision making in prey (Skalski and Gilliam 2002). Alonzo's (2002) model considered that energy reserves affect prey fitness and predicted that prey should favour the habitat with more resources if their energy reserves are low (i.e., if the risk of starvation is high), but that prey distribution would be unaffected by resource distribution if their energy reserves are high. Given that dace were fed *ad libitum* each day, we had no reason to predict that dace would select the richer patch because their risk of starvation was high.

Because there was no food in the plastic grid tunnel between the two feeding patches, we expected that dace would mainly use the patches to forage and use the plastic grid tunnel only to move from one patch to the other. However, in the presence of creek chub (experiments *c* and *f*), dace used the patches less often and their movements between patches were reduced compared to experiments without creek chub (A. Dupuch; pers. observ.). Accordingly, the mean number of dace observed per minute in the two patches combined was significantly lower in experiments with than without creek chub (Fig. 6). Furthermore, when creek chub were free to move between patches (experiment *f*), the proportion of dace leaving the feeding patches to take refuge in the tunnel increased significantly with the mean number of chub observed per minute in the feeding patches (Fig. 7). Sih (1984) also showed that in the presence of a refuge, prey distribution was negatively related to predator distribution, with prey avoiding areas with numerous predators, and that prey movements decreased as predator movements increased. In fact, in addition to the two feeding patches, the tunnel offered a third, totally safe area for dace, but without food. After the introduction of creek chub, our results suggest that dace reduced their use of the least complex patch in favour of the refuge habitat (i.e., the tunnel) or the

more structurally complex feeding patch. As the number of creek chub in the patches increased, dace aggregated and stayed motionless in the tunnel to avoid them.

Similarly, Gilliam and Fraser (1987) studied juvenile creek chub (prey) habitat selection among a refuge habitat and two feeding areas in which predation risk (i.e., the number of adult piscivorous creek chub) and resource levels were varied experimentally. As in our experiment, juvenile creek chub (prey) spent significantly more time in the refuge habitat as the number of adult creek chub (predator) increased in the feeding areas. Although we always introduced seven creek chub to the experimental tank (experiment *f*), the predation risk intensity likely varied from one experiment to another, due to variation in the activity level of creek chub and the attack rate on dace. Indeed, the number of predation events occurring during a trial varied and significantly increased with the mean number of chub observed per minute in the two patches combined, but significantly decreased with the mean number of dace observed there. This result suggests that dace used the refuge habitat more often as the overall level of predation risk in the experimental tank increased. Therefore, given the use of the refuge habitat (relative to both feeding patches), our results suggest that dace considered inherent habitat riskiness as being more important than resource distribution as predation risk intensity increased.

These results support the prediction of Luttbeg and Sih's model (2004). Their model predicts that if prey fitness is body-mass dependent (which is often the case), the relative contribution of resources and riskiness in determining prey distribution depends on the level of predation risk. When the level of predation risk is low, their model predicts that prey should favour the richer habitat even if it is the inherently riskier one. But when the level of predation risk is high, prey distribution should be mainly determined by the habitat riskiness ratio. Both the models of Hugie and Dill (1994) and Sih (1998) predict that the influence of resource distribution on prey distribution should increase with competition among predators. Given that in these models, an increase in competition among predators decreases the predation risk of prey, both models also indirectly predict that the importance of resource distribution

in prey distribution is inversely related to the level of predation risk. As in our study, the intensity of predation risk would also explain the variations of distribution between habitats differing in inherent riskiness in rodent (*Dipodomys* spp.; the prey) in response to snake (*Crotalus cerastes*; the predator) distribution (Bouskila 2001), and in bottlenose dolphins (*Tursiops aduncus*), dugong (*Dugong dugon*), and pied cormorants (*Phalacrocorax varius*) in response to tiger shark (*Galeocerdo cuvier*) distribution (Heithaus and Dill 2002; Heithaus 2005; Heithaus and Dill 2006; Wirsing *et al.* 2007).

In conclusion, the use by dace of the refuge habitat (relative to both feeding patches) suggests that the influence of resource distribution and inherent habitat riskiness on prey distribution varies with the level of predation risk. In fact, the more numerous the creek chub were in the two patches combined, the more dace aggregated in the refuge habitat. Thus, predator avoidance seems to determine habitat choice of dace as predation risk increases. In accordance with these results, a negative correlation between prey and predator distribution has commonly been observed (Sih 1984; Bouskila 2001; Sih 2005; Hammond *et al.* 2007), regardless of habitat characteristics (i.e., resource quantity and inherent habitat riskiness). This suggests that predator avoidance has a stronger effect on habitat selection by prey than resource distribution, inherent habitat riskiness or conspecific avoidance (see also Hammond *et al.* 2007). On the other hand, when dace were outside the refuge habitat, they considered resource quantity and, to a lesser extent, inherent habitat riskiness when choosing a feeding patch. This suggests that when prey accept the risk imposed by predators, foraging success rather than mortality risk drives their habitat choice.

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Table 1: Results of the general linear model to test for the effects of inherent habitat riskiness and food proportion on the proportion of dace in patch 1, with and without creek chub in the experimental tank (i.e., experiments *e* and *f*).

Model Variables	Estimate	df	F-value	P-value	Partial R^2	R^2 model
Without predators		2	60.38	< 0.001		0.70
Intercept	55.92					
Food proportion	-19.43	1	115.75	< 0.001	0.68	
Habitat riskiness	-2.03	1	5.01	0.029	0.02	
Food prop. x habitat risk.				NS		
With predators		2	21.78	< 0.001		0.48
Intercept	53.28					
Food proportion	-18.78	1	30.79	< 0.001	0.34	
Habitat riskiness	-6.07	1	12.76	< 0.001	0.14	
Food prop. x habitat risk.				NS		

Table 2: Mean proportion of dace in patch 1 (with 95% CI) for each combination of food proportion x inherent habitat riskiness ratio during the experiment without predators (experiment *e*). Bold characters indicate that the mean proportion of dace in patch 1 did not differ from an IFD (CI included the expected value from the IFD, i.e., 75 and 25, respectively).

Food proportion in patch 1	Inherent habitat riskiness ratio (patch 1/patch 2)				
	1/3	1/2	1/1	2/1	3/1
75%	**60(41-79)**	55(41-69)	**57(33-81)**	54(46-61)	56(42-70)
25%	39(29-48)	42(29-54)	36(29-44)	**34(17-51)**	**31(2-61)**

Table 3: Results of the general linear model to test for the effects of inherent habitat riskiness, food proportion and their interactions with predation risk (creek chub absent or present) on the proportion of dace in patch 1 (i.e., experiments *e vs. f*).

Variables	Estimate	df	F-value	P-value	R^2
Full model		5	24.56	< 0.001	0.56
Intercept	53.28				
Food proportion	-18.78	1	99.20	< 0.001	
Habitat riskiness	- 6.06	1	17.69	< 0.001	
Predator	2.64	1	1.46	0.231	
Habitat riskiness x predator	4.03	1	4.40	0.038	
Food proportion x predator				NS	

Figure captions

Figure 1: (a) Diagram of the two experimental tanks. The tunnel between the two feeding patches, the vertical partitions and the circular partitions around the feeders (all made of plastic grid) allowed northern redbelly dace but not creek chub to pass. The vertical partitions were present only in experiment *c*. The tunnel and the circular partitions around the feeders were present in all the experiments. (b) Lateral view of one experimental tank with different straw densities, which create variable habitat riskiness in the two feeding patches. Containers collecting trout pellets not eaten by fish were present in all the experiments.

Figure 2: Variations in the proportion of dace (a) and creek chub (b) in patch 1 according to the proportion of food delivered in patch 1 (experiments *a* and *b*, respectively). On the X axis, 14%, 25%, 50%, 75% and 86% correspond to the following food ratios (patch 1: patch 2): 1:6, 1:3, 1:1, 3:1 and 6:1, respectively. Dashed lines represent the expected perfect match between resource distribution and the spatial distribution of fish under an Ideal Free Distribution model. Data are means ± S.E.

Figure 3: Variations in the proportion of dace in patch 1 according to the proportion of creek chub in patch 1 (experiment *c*). On the X axis, 14%, 28%, 43%, 57%, 71% and 85% correspond to the following creek chub ratios (patch 1: patch 2): 1:6, 2:5, 3:4, 4:3, 5:2 and 6:1, respectively. Data are means ± S.E.

Figure 4: Variations in the proportion of dace in patch 1 according to the inherent habitat riskiness ratio (experiment *d*). On the X axis, 0.33, 0.5, 1, 2, and 3 correspond to the following inherent habitat riskiness ratios (patch 1: patch 2): 1:3, 1:2, 1:1, 2:1 and 3:1, respectively. Data are means ± S.E.

Figure 5: Variations in the proportion of dace in patch 1 according to the inherent habitat riskiness ratio and proportion of food in patch 1 (white symbols = 25%, black symbols = 75%) in the absence (circles: experiment *e*) or presence (squares: experiment *f*) of creek chub (groups of seven individuals per trial). On the X axis, 0.33, 0.5, 1, 2, and 3 correspond to the following inherent habitat riskiness ratios (patch 1: patch 2): 1:3, 1:2, 1:1, 2:1 and 3:1, respectively. Data are means ± S.E. See text and Tables 1 and 3 for statistics.

Figure 6: Box plot representing the mean number of dace observed per minute in the two feeding patches combined during a trial for experiments *a*, *c*, *d*, *e* and *f*. Cross indicates experiments in which creek chub were present. 1 and 2 refer to the periods before and after the introduction or the mimicked introduction of the creek chub, respectively. Experiments accompanied by different capital letters were significantly different ($p < 0.001$).

Figure 7: Variations in the proportion of dace in the tunnel after introduction of creek chub in the experimental tank (experiment *f*) according to the mean number of chub observed per minute in the two feeding patches.

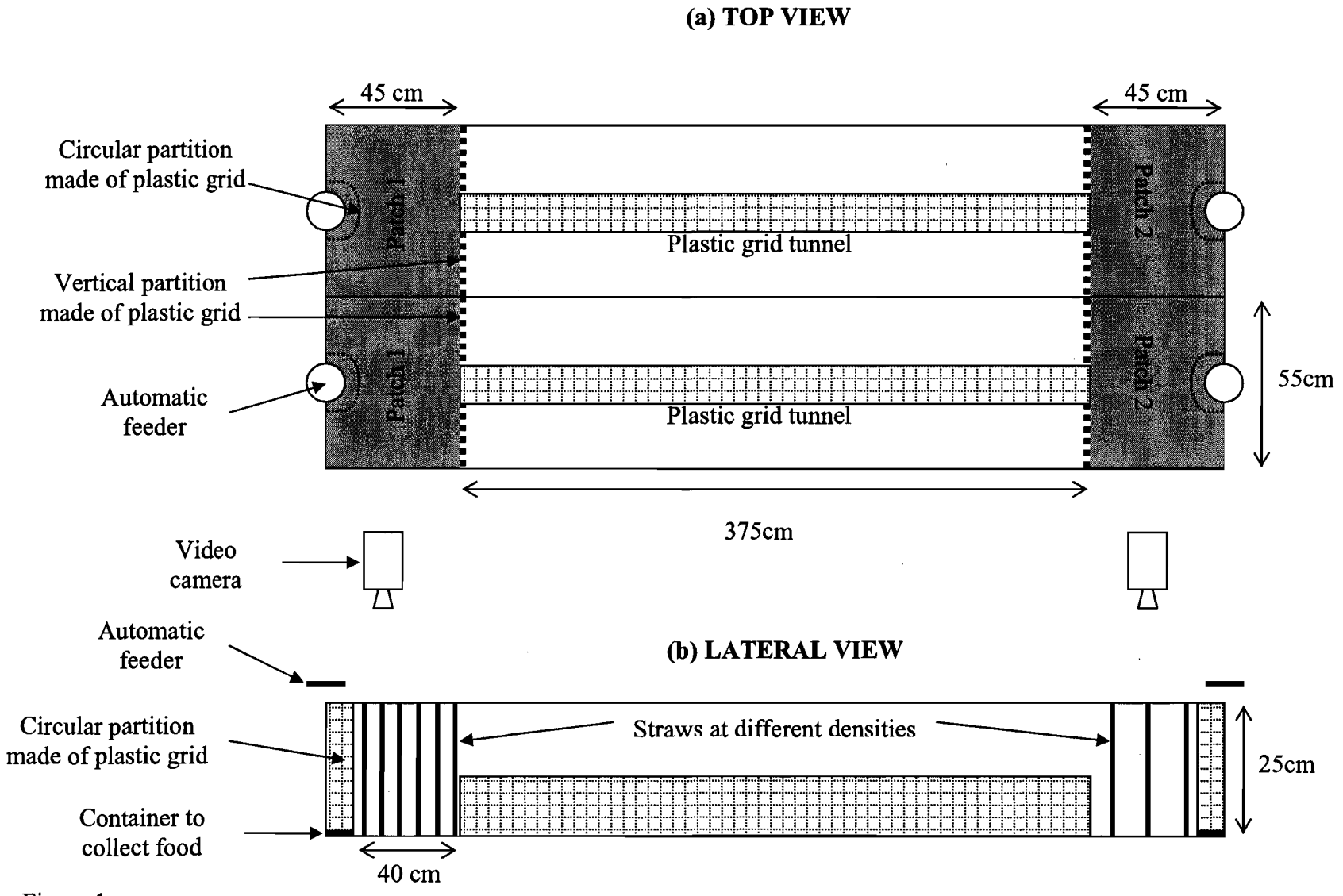
(a) TOP VIEW
45 cm
45 cm
Circular partition made of plastic grid
Vertical partition made of plastic grid
Automatic feeder
Patch 1
Patch 1
Patch 2
Patch 2
Plastic grid tunnel
Plastic grid tunnel
55cm
375cm
Video camera
Automatic feeder
(b) LATERAL VIEW
Circular partition made of plastic grid
Container to collect food
Straws at different densities
25cm
40 cm

Figure 1

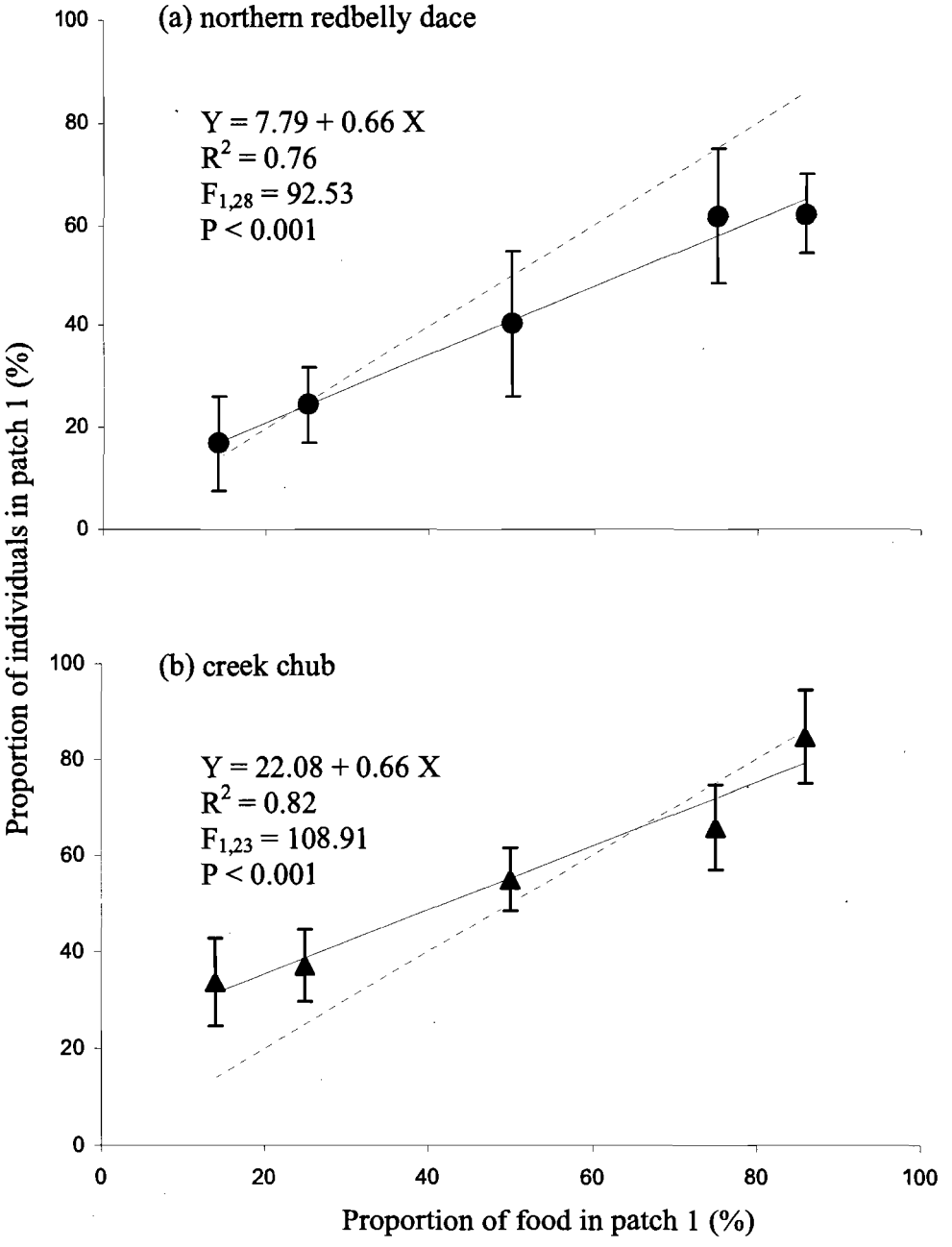
(a) northern redbelly dace
Y = 7.79 + 0.66 X
R^2 = 0.76
$F_{1,28}$ = 92.53
P < 0.001
(b) creek chub
Y = 22.08 + 0.66 X
R^2 = 0.82
$F_{1,23}$ = 108.91
P < 0.001
Proportion of individuals in patch 1 (%)
Proportion of food in patch 1 (%)
0
20
40
60
80
100

Figure 2

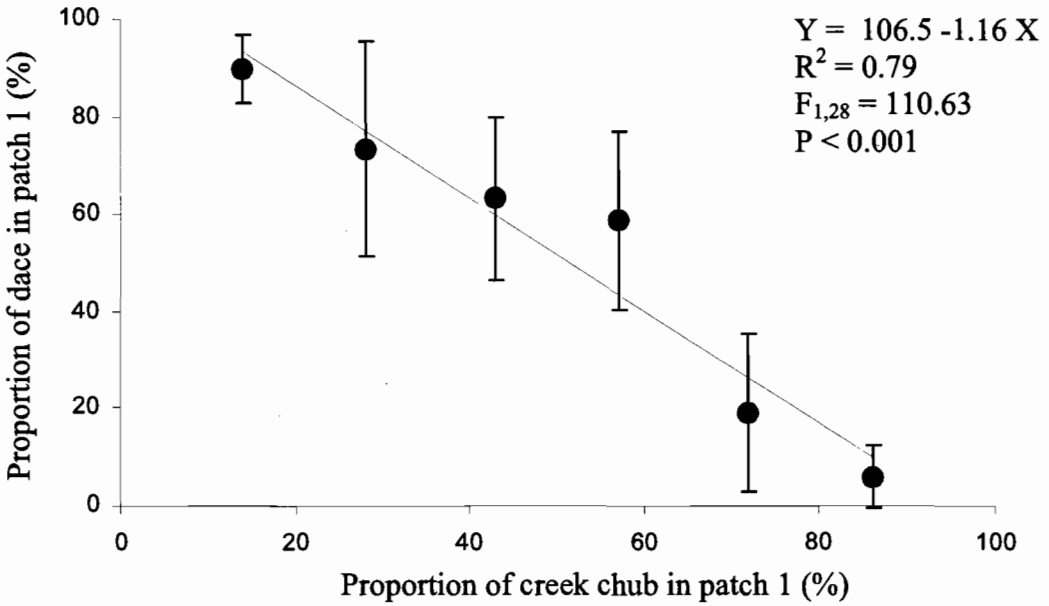
Y = 106.5 -1.16 X
R^2 = 0.79
$F_{1,28}$ = 110.63
P < 0.001
Proportion of dace in patch 1 (%)
Proportion of creek chub in patch 1 (%)
0
20
40
60
80
100

Figure 3

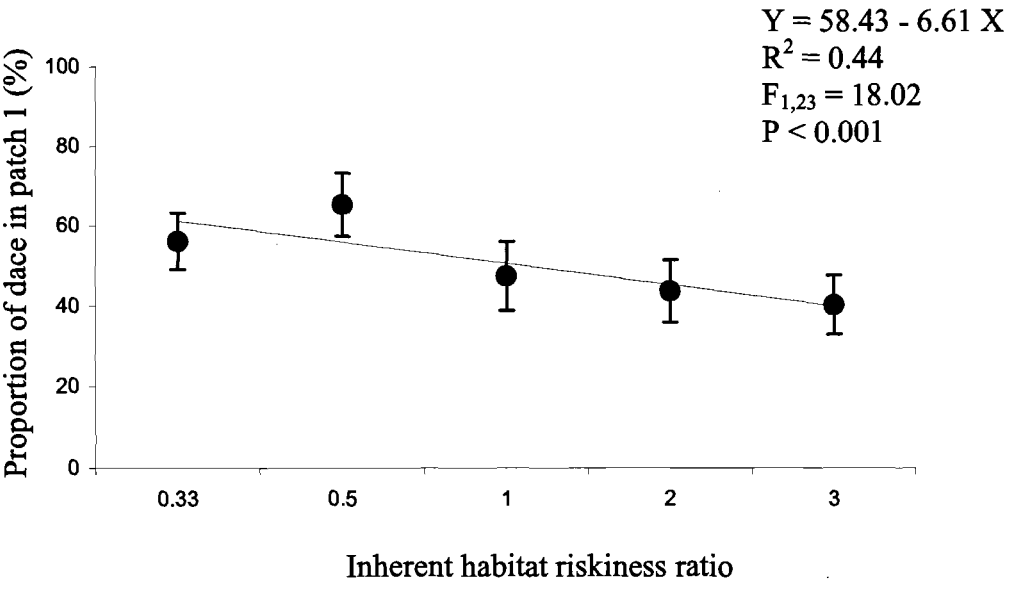
Y = 58.43 - 6.61 X
$R^2 = 0.44$
$F_{1,23} = 18.02$
$P < 0.001$
Proportion of dace in patch 1 (%)
100
80
60
40
20
0
0.33
0.5
1
2
3
Inherent habitat riskiness ratio

Figure 4

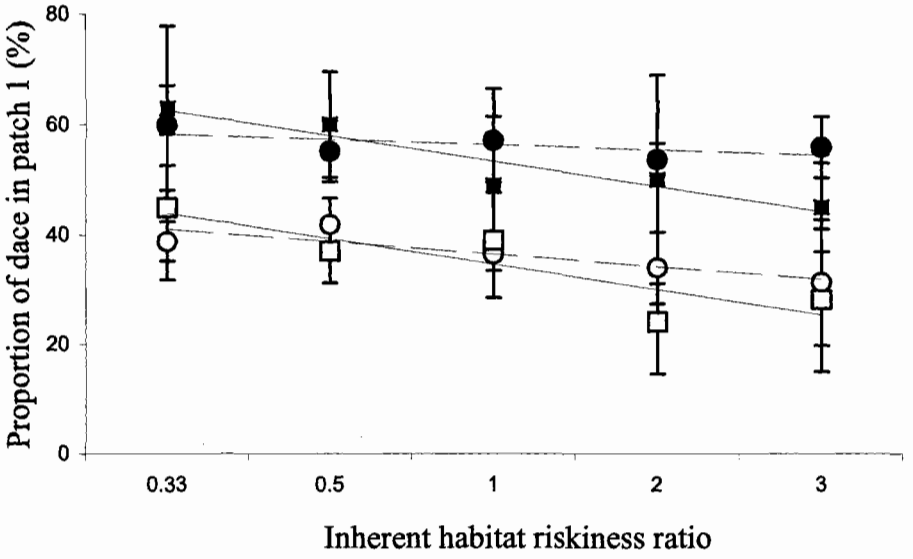
Proportion of dace in patch 1 (%)
80
60
40
20
0
0.33
0.5
1
2
3
Inherent habitat riskiness ratio

Figure 5

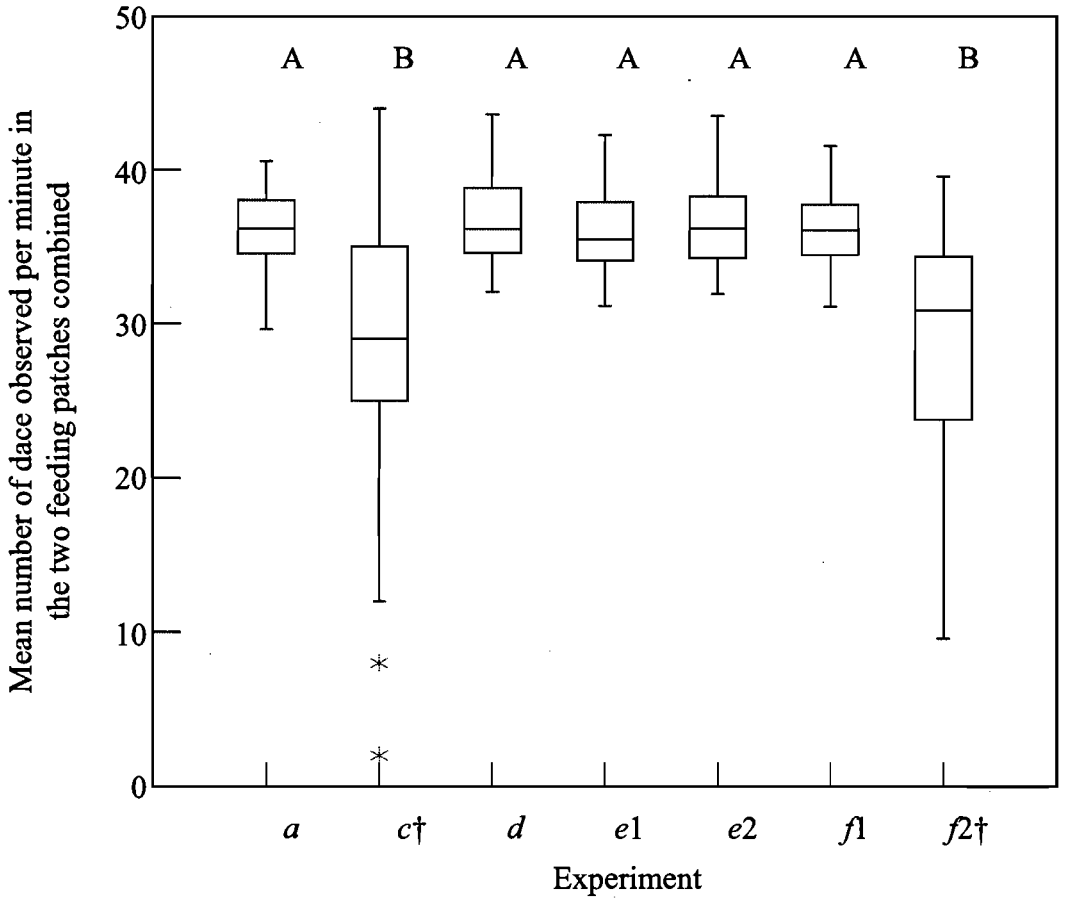
Mean number of dace observed per minute in the two feeding patches combined
50
40
30
20
10
0
A
B
A
A
A
A
B
a
c†
d
e1
e2
f1
f2†
Experiment

Figure 6

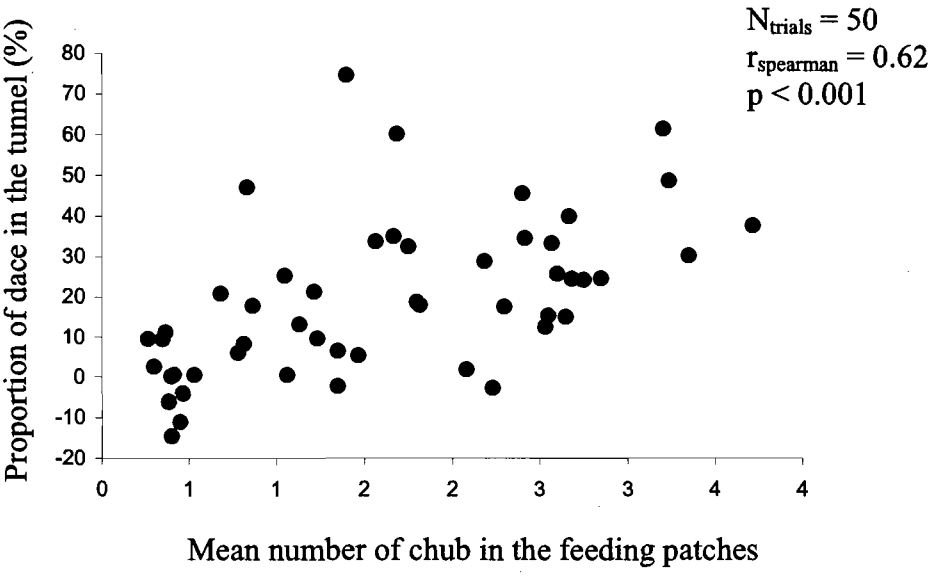
$N_{trials} = 50$
$r_{spearman} = 0.62$
$p < 0.001$
Proportion of dace in the tunnel (%)
80
70
60
50
40
30
20
10
0
-10
-20
0
1
1
2
2
3
3
4
4
Mean number of chub in the feeding patches

Figure 7

DISCUSSION GÉNÉRALE

Cette thèse s'est intéressée au comportement et à la sélection de l'habitat par une espèce-proie, le ventre rouge du nord (*Phoxinus eos*), lorsqu'elle est confrontée à un risque de prédation qui varie en intensité, dans le temps et dans l'espace. Beaucoup d'études se sont penchées sur l'utilisation des habitats par les prédateurs et les proies, mais la plupart d'entre elles ont exploré le comportement des prédateurs et des proies en fixant l'un ou l'autre dans l'espace. Les connaissances théoriques et empiriques sur l'utilisation des habitats par les prédateurs et les proies quand les deux peuvent se déplacer librement sont peu abondantes.

Perception du risque de prédation et réponse anti-prédateur

Un grand nombre d'études ont montré qu'un animal qui doit prendre une décision d'ordre comportemental considère le risque de prédation associé à cette décision (Lima et Dill 1990; Lima 1998). Une telle habileté implique que l'animal a des informations spatio-temporelles fiables sur le risque de prédation. Les indices chimiques constituent une source importante d'informations, en révélant la présence de prédateurs (ou leur passage récent), et en donnant des renseignements sur le taux d'activité du prédateur et son alimentation (Kats et Dill 1998; Wisenden 2000; Brown 2003). Les réponses comportementales à court terme des proies aux signaux d'alarme ont reçu beaucoup d'attention de la part des chercheurs et ressemblent à celles exprimées par les individus en présence de prédateurs (Chivers et Smith 1998). Notre étude a montré que les ventres rouges du nord répondaient à des extraits de peau de congénères par un ensemble de comportements anti-prédateur (Chapitre I); les individus se rapprochaient du substrat et s'éloignaient de la zone d'injection de la substance chimique d'alerte, augmentaient la cohésion et la polarisation du banc, et faisaient plus de mouvements brusques et d'immobilisations prolongées. Ces réponses comportementales, très largement observées chez les poissons-proie

(Chivers et Smith 1998), ont pour effet de rendre les proies plus difficiles à capturer pour les prédateurs (Smith 1997). Le ventre rouge du nord, comme de nombreuses autres espèces-proie, pourrait ainsi utiliser cette sensibilité à la substance chimique d'alerte pour estimer le risque de prédation en nature (Kats et Dill 1998; Brown 2003).

Les organismes se basant sur les indices chimiques pour estimer le risque de prédation devraient être capables d'utiliser les gradients chimiques pour avoir une meilleure estimation du risque de prédation. Les proies ayant une telle capacité d'adaptation pourraient ainsi optimiser le compromis entre la réduction du risque de prédation et les bénéfices associés à toute autre activité reliée à la valeur adaptative (Lima et Dill 1990), en adaptant leur comportement en fonction de l'intensité du risque de prédation (Helfman 1989). Conformément à cette hypothèse, notre étude a montré que l'intensité des réponses comportementales du ventre rouge du nord était directement corrélée à la concentration de la substance chimique d'alerte, ce qui indique que cette espèce est capable d'adapter l'intensité de sa réponse anti-prédateur au degré du risque de prédation. Le fait que les ventres rouges du nord évitaient d'autant plus un habitat quand ce dernier contenait un nombre croissant de prédateurs (Chapitre IV) corrobore ce résultat.

Sélection de l'habitat et variations du risque de prédation

À l'échelle du lac

Bien que les migrations nycthémérales (verticales et horizontales) entre deux habitats aient fait l'objet d'un grand nombre d'études, ni les facteurs proximaux ni les mécanismes expliquant ces migrations ne sont pleinement compris (Gliwicz 2003). L'évitement des prédateurs est le mécanisme le plus souvent cité pour expliquer les migrations nycthémérales horizontales (p. ex., Naud et Magnan 1988; Gliwicz et Jachner 1992; Brabrand et Faafeng 1993). Cependant, cette hypothèse n'a jamais été rigoureusement testée due à la difficulté de mesurer le risque de prédation en nature.

L'utilisation de proies vivantes et attachées dans des environnements différents est une bonne méthode pour obtenir une mesure du risque relatif de prédation dans des habitats contrastés (Aronson et Heck 1995). Cette méthode intègre les variations spatiales et temporelles de la densité des prédateurs et de leur activité alimentaire (Post et al. 1998). Les expériences d'attachement conduites en milieu naturel ont montré que les patrons spatiaux et temporels du risque relatif de prédation du ventre rouge du nord étaient hétérogènes en lac (Chapitre II). En effet, la zone la plus dangereuse pour le ventre rouge du nord était la zone pélagique profonde, suivie de la zone littorale, puis de la zone pélagique supérieure. Cependant, notre étude a probablement surestimé le risque relatif de prédation dans la zone littorale, en plaçant, pour des raisons logistiques, les ventres rouges du nord dans des zones ne contenant aucune structure. Durant la journée, la zone littorale est probablement la zone la plus sécuritaire pour le ventre rouge du nord, dû à la présence de végétation et de structures ligneuses submergées que les individus utilisent de manière préférentielle (p. ex., Naud et Magnan 1988; He et Lodge 1990; Jacobus et Ivan 2005). En laboratoire, l'utilisation de tels habitats a permis aux individus de réduire significativement le nombre d'attaques et de captures par l'omble de fontaine (East et Magnan 1991).

L'hypothèse que la zone littorale est utilisée comme refuge par le ventre rouge du nord est également supportée par la corrélation positive et significative entre l'abondance des ventres rouges du nord dans la zone littorale et le risque relatif de prédation en zone pélagique des lacs étudiés (Chapitre III). Ce résultat est cohérent avec celui de Gaudreau et Boisclair (1998) qui ont montré que l'abondance du ventre rouge du nord en dehors de la zone littorale des lacs est réduite dans les lacs contenants des prédateurs pélagiques. En plus de la proximité d'habitats structurés, la faible présence de l'omble de fontaine dans la zone littorale (Bourke *et al.* 1996) pourrait contribuer à expliquer la préférence du ventre rouge du nord pour la zone littorale durant la journée. Ces deux hypothèses sont supportées par les résultats des expériences effectuées en laboratoire (Chapitre IV), montrant que les ventres rouges

du nord (i) évitaient les habitats contenant de nombreux prédateurs et (ii) augmentaient l'utilisation des habitats fortement structurés en présence de prédateurs (en comparaison avec les expériences sans prédateurs).

En comparant différents lacs, nous avons montré que la présence du mulet à cornes et du meunier noir a influencé le patron spatial du risque relatif de prédation, mais pas son intensité globale (Chapitre II). Le risque relatif de prédation du ventre rouge du nord a augmenté dans les zones littorale et pélagique supérieure, mais a diminué dans la zone pélagique profonde en présence du mulet et du meunier par rapport aux lacs où l'omble de fontaine était la seule espèce présente. Ces résultats sont cohérents avec ceux d'études précédentes (Magnan et Fitzgerald 1982; Tremblay et Magnan 1991) qui ont montré que la distribution spatiale de l'omble de fontaine en lac se déplaçait de la zone benthique vers la zone pélagique en présence de mulets à cornes et de meuniers noirs. D'autre part, la prédation inattendue du mulet sur le ventre rouge du nord (A. Dupuch, observation personnelle) expliquerait en partie l'augmentation du risque relatif de prédation dans la zone littorale, observé dans les lacs avec compétiteurs (Chapitre II). Au niveau temporel, le risque de prédation était significativement plus faible la nuit que le jour, toutes zones confondues. Le fait que l'omble de fontaine soit un prédateur visuel (Power 1980) expliquerait ce résultat. Cette étude montre donc que l'intensité lumineuse, la composition spécifique et la position spatiale (via les effets de la distribution spatiale des prédateurs et des différences de complexité structurelle entre les zones) sont d'importants déterminants du risque relatif de prédation du ventre rouge du nord.

Les résultats des expériences d'attachement offrent un support quantitatif à l'hypothèse que l'évitement des prédateurs serait le mécanisme expliquant les migrations nycthémérales. Durant le jour, les ventres rouges du nord utiliseraient la zone littorale pour réduire leur risque de prédation par l'omble de fontaine, un prédateur visuel, et en sortiraient principalement la nuit, parce que le risque de prédation est faible dans l'ensemble du lac à cette période. Ces migrations nocturnes vers la zone pélagique sont associées à une augmentation de la consommation de

zooplancton par le ventre rouge du nord (Gauthier et Boisclair 1997; A. Dupuch, données non publiées) et coïncident avec une forte abondance de zooplancton dans la zone pélagique supérieure (Naud et Magnan 1988; Gauthier et Boisclair 1997; Annexe A). L'ensemble de ces résultats supporte l'hypothèse que ces migrations nycthémérales permettraient au ventre rouge du nord de réduire son risque de prédation tout en maximisant son taux d'alimentation sur le zooplancton, et suggère que la luminosité et la complexité structurelle de l'habitat sont des facteurs proximaux importants dans l'explication de ces migrations (Chapitre III). Ces résultats supportent également les prédictions du modèle théorique de Lima et Bednekoff (1999), montrant que la variabilité temporelle du risque de prédation confronte les animaux au problème de la répartition des efforts à s'alimenter et à éviter d'être la victime d'un prédateur à travers les différentes périodes du risque de prédation (i.e., faible *versus* élevé). Leurs résultats suggèrent qu'un animal devrait consacrer plus d'efforts aux comportements anti-prédateurs durant les périodes où le risque de prédation est élevé et plus d'efforts à s'alimenter pendant les périodes où le risque de prédation est faible. En accord avec cette prédiction, les ventres rouges du nord s'alimentent principalement la nuit (Gauthier et Boisclair 1997; A. Dupuch, données non publiées), et adoptent des comportements anti-prédateurs le jour (i.e., la vie en banc, préférence pour la zone littorale qui est faible en prédateurs et riche en habitats structurés).

À l'échelle de la zone littorale

Les proies passent souvent plus de temps et sont souvent plus nombreuses dans les habitats structurés en réponse au risque de prédation (Lima et Dill 1990; Lima 1998). En accord avec cette théorie, l'abondance des ventres rouges du nord était en moyenne significativement plus élevée dans les habitats structurés que dans les habitats sans structure de la zone littorale (Chapitre III), un patron de distribution déjà observé dans d'autres études (p. ex., Naud et Magnan 1988; He et Lodge 1990; Jacobus et Ivan 2005). Cependant, la proportion de ventre rouge du nord dans les

habitats structurés de la zone littorale était négativement corrélée avec leur risque relatif de prédation (Chapitre III). Ce résultat ne contredit pas l'hypothèse que les ventres rouges du nord utilisent la végétation et les structures ligneuses pour réduire leur risque de prédation (Naud et Magnan 1988; Gauthier et Boisclair 1997). En fait, les poissons-proies n'augmentent pas toujours leur utilisation des habitats structurés en présence de prédateurs (p. ex., Jacobsen et Berg 1998; Pink *et al.* 2007). D'une part, chez le ventre rouge du nord, l'utilisation des eaux peu profondes semble être une alternative à l'utilisation des habitats structurés comme refuge (He 1986). D'autre part, en réponse au risque de prédation, le comportement de banc peut être préféré à l'utilisation des habitats structurés. Cela a été démontré chez le ventre rouge du nord dans la zone littorale de lacs (Pink *et al.* 2007), et chez le gardon (*Rutilus rutilus*) dans des bassins expérimentaux (Jacobsen et Berg 1998). Le comportement de banc permet aux individus de chercher leur nourriture en se déplaçant d'un habitat à un autre tout en réduisant leur risque de prédation (Pitcher et Parrish 1993; Eklov et Persson 1995; Godin 1997), alors que se cacher dans un refuge est souvent associé à une augmentation de la compétition à l'intérieur du refuge et à une perte de temps qui n'est pas consacré à alimentation (Werner *et al.* 1983; Sih 1997). Ainsi, la flexibilité des tactiques anti-prédateurs observée chez le ventre rouge du nord expliquerait leur distribution inattendue entre les habitats structurés et sans structure de la zone littorale.

Facteurs déterminants le choix de l'habitat par les proies

L'effet conjoint de la distribution de la ressource alimentaire et du risque inhérent à l'habitat sur la sélection de l'habitat par les prédateurs et les proies n'a fait l'objet que d'études théoriques. Ces modèles théoriques prédisent que la distribution des proies ne devrait pas (ou presque pas) être influencée par la distribution de la ressource alimentaire. De plus, si le risque inhérent à l'habitat varie, les modèles prédisent que la distribution des proies devrait être principalement influencée par le

risque inhérent à l'habitat, les proies évitant les habitats les plus risqués, quelle que soit la distribution de la ressource alimentaire (Hugie et Dill 1994; Sih 1998; Luttbeg et Sih 2004). Nos résultats expérimentaux (Chapitre IV) ont montré qu'en absence de prédateurs, la distribution spatiale des ventres rouges du nord était positivement et essentiellement reliée à la distribution spatiale de la ressource alimentaire. Cependant, les résultats des expériences avec des prédateurs libres de se déplacer indiquent (i) que l'influence de la distribution de la ressource et du risque inhérent à l'habitat sur la distribution des ventres rouges du nord diminue et augmente respectivement avec l'intensité du risque de prédation, et (ii) que l'évitement des prédateurs détermine le choix de l'habitat par les ventres rouges du nord quand le risque de prédation est élevé. Ainsi, ces résultats indiquent que l'importance relative des facteurs dans la sélection de l'habitat par la proie dépend de l'intensité du risque de prédation, ce qui concorde avec les prédictions du modèle de Luttbeg et Sih (2004). D'autre part, le fait que l'évitement des prédateurs détermine le choix de l'habitat par les proies est cohérent avec la corrélation négative souvent observée entre la distribution des prédateurs et des proies (Sih 1984; Bouskila 2001; Sih 2005; Hammond *et al.* 2007), quelles que soient les caractéristiques de l'habitat (i.e., la quantité de ressource ou le risque inhérent à l'habitat). Ceci suggère que l'évitement des prédateurs a un effet plus important sur la sélection de l'habitat des proies que la distribution des ressources, le risque inhérent à l'habitat ou l'évitement des congénères (voir aussi Hammond *et al.* 2007).

Ces résultats sont cohérents avec le comportement du ventre rouge du nord en lac. En effet, quand le risque de prédation est élevé (i.e., durant la journée), les ventres rouges du nord utilisent principalement la zone littorale, qui offre plus de refuges et qui est plus pauvre en prédateurs (i.e. omble de fontaine) que la zone pélagique (Tremblay et Magnan 1991; Bourke *et al.* 1996), et utilisent peu la zone pélagique pourtant plus riche en zooplancton (i.e., en ressource alimentaire) que la zone littorale (Annexe A; Naud et Magnan 1988; Gauthier et Boisclair 1997). Cependant, quand le risque de prédation est faible (i.e., la nuit) les ventres rouges du

nord migrent massivement vers la zone pélagique pour s'alimenter sur le zooplancton.

Application des modèles théoriques

Cette étude s'est intéressée à la prédiction de modèles de sélection de l'habitat par les proies qui considèrent les prédateurs comme étant libre de se déplacer et de poursuivre leur proie dans l'espace (Chapitre IV). Il existe également des modèles considérant le risque de prédation comme étant fixé dans l'espace, i.e. qu'un habitat est toujours plus risqué que l'autre (le prédateur n'est présent que dans un seul habitat ; p. ex., Moody *et al.* 1996). Ces deux approches peuvent s'appliquer à toute situation dans laquelle les proies sont mobiles et doivent choisir entre deux habitats d'alimentation qui diffèrent en terme de quantité de ressource et de risque de prédation (incluant le risque inhérent à l'habitat et la présence de prédateurs). Cependant, les modèles considérant le risque de prédation comme étant fixé dans l'espace s'appliqueraient plus aux systèmes naturels où les proies sont les victimes de nombreuses espèces de prédateurs, de prédateurs généralistes, ou de prédateurs chassant uniquement dans un type spécifique d'habitat. À l'inverse, la sélection de l'habitat dans un contexte de jeu entre les prédateurs et les proies s'appliquerait plus aux systèmes naturels où les proies sont victimes d'une seule espèce de prédateur mobile (p. ex., Heithaus et Dill 2002; Heithaus 2005; Heithaus et Dill 2006; Wirsing *et al.* 2007). D'une manière générale, cette approche s'appliquerait plutôt aux systèmes pauvres en espèces (et donc pauvres en prédateurs) tels que les systèmes désertique ou polaire. Par exemple, la distribution spatiale des rongeurs (*Dipodomys* spp.; la proie) et des crotales (*Crotalus cerastes*; le prédateur) entre des habitats avec et sans structure dans le désert (Bouskila 2001), aisni que celle du krill et des pingouins de l'antarctique (Alonzo *et al.* 2002) en sont de bons exemples. Les migrations verticales journalières observées chez le zooplancton et les poissons zooplanctivores illustrent également bien le jeu existant entre les prédateurs et les

proies dans la sélection de l'habitat (Iwasa 1982). Dans de tels systèmes, le risque inhérent à l'habitat varie dans le temps (ici, avec l'intensité lumineuse), résultant en une sélection de l'habitat très dynamique. Les migrations horizontales journalières entre les zones littorale et pélagique observées chez le ventre rouge du nord et d'autres espèces de poisson d'eau douce (p. ex., la chatte de l'est, *Notemigonus crysoleucas,* Hall *et al.* 1979; le gardon, *Rutilus rutilus*, Gliwicz et Jachner 1992) sont également des systèmes qui pourraient être étudiés dans la perspective d'un jeu entre prédateurs et proies (Hugie et Dill 1994).

Sélection de l'habitat, risque de prédation et conservation

L'étude de la sélection de l'habitat par les animaux permet entre autres de comprendre les besoins d'une espèce en terme d'habitat, ce qui est une première nécessité dans tout programme de conservation (Sutherland 1998; Caro et Eadie 2005). De plus, la détermination des facteurs influençant l'utilisation des habitats par les organismes (et donc les règles de décision liée à la sélection de l'habitat) est importante pour prédire les impacts des changements anthropiques sur l'environnement et peut permettre d'appliquer des plans de gestion, de restauration ou de conservation efficaces (p. ex., Torres *et al.* 2006). Les modèles basés sur la Distribution Idéale et Libre peuvent donc s'avérer très utiles pour déterminer les habitats essentiels à une espèce, ainsi que les effets de la perte d'habitats et de la diminution de la ressource alimentaire sur la distribution spatiale et l'abondance de cette espèce (p. ex., Stillman *et al.* 2000, 2001). D'autre part, le fait que pratiquement tous les animaux sont des proies potentielles pour d'autres animaux justifie l'étude de l'effet du risque de prédation sur la sélection de l'habitat par les organismes. De plus, dans un contexte de conservation, cela est d'autant plus pertinent que beaucoup de perturbations anthropiques (p. ex., la simple présence de l'homme ou des bruits dus à des véhicules motorisés) sont perçues comme un risque de prédation par les organismes. En effet, ces derniers adaptent leur comportement de la même manière

face à un prédateur que face à une perturbation causée par l'homme (Frid et Dill 2002).

Conclusion générale

Les connaissances actuelles concernant la sélection de l'habitat par les proies lorsqu'elles sont en présence de prédateurs libres de se déplacer reposent sur peu d'études. Les études empiriques sont rares et aucune ne s'est intéressée à l'effet conjoint de la distribution de la ressource alimentaire et du risque inhérent à l'habitat sur la sélection de l'habitat par les proies. Dans ce contexte, les résultats de ce projet de doctorat sont en partie uniques et devraient aider à comprendre les décisions comportementales reliées à la sélection de l'habitat par les proies dans les systèmes où les prédateurs peuvent ajuster leur distribution à celle des proies. Ce projet de doctorat a montré que dans les systèmes où le risque de prédation varie en intensité, dans le temps et dans l'espace (ce qui est certainement le cas dans la plupart des systèmes naturels), (i) les réponses et les tactiques anti-prédateurs des proies peuvent être flexibles, (ii) les proies adoptent des comportements anti-prédateurs dans les situations où le risque de prédation est élevé, et s'alimentent dans les situations de faible risque de prédation, et (iii) l'évitement des habitats risqués (i.e., riches en prédateurs et/ou pauvres en refuges) détermine le choix de l'habitat des proies dans les situations où le risque de prédation est élevé. Il en résulte une sélection dynamique de l'habitat par les proies, qui peut se traduire en milieu naturel, par une forte variabilité spatiale et temporelle de leurs patrons de distribution (p. ex., les migrations nycthémérales).

Perspectives de recherche

Perception et estimation du risque de prédation

Les quantités de substances chimiques d'alerte réellement présentes dans l'environnement et la durée pendant laquelle ces substances restent actives en nature ne sont pas connues. De plus, d'autres sources d'information peuvent être utilisées par les poissons-proie pour estimer le risque de prédation, telles que des facteurs associés à l'environnement (p. ex., la luminosité, la complexité structurelle des habitats; Chapitre IV) ou aux prédateurs (p. ex., leur taille, leur densité; Chivers *et al.* 2001). La façon dont les organismes intègrent ces différentes informations pour estimer le risque de prédation reste à être déterminée. Par conséquent, l'estimation de (i) l'importance relative des indices chimiques dans l'estimation du risque de prédation par les proies, et (ii) du risque de prédation perçu par les proies seront des défis pour les recherches futures.

Flexibilité de la réponse anti-prédateur

La sensibilité des individus au degré du risque de prédation a été démontrée chez un grand nombre d'espèces (Brown *et al.* 2006). Cependant, les résultats de plusieurs études récentes montrent qu'il existe une variation inter- et intraspécifique considérable, les individus montrant des réponses anti-prédateurs du type "intensité graduelle" (i.e., flexible) à des réponses du type "tout ou rien" (i.e., rigide) (p. ex., Zhao et Chivers 2005; Brown et al. 2006). Les facteurs déterminant la forme de la réponse restent à être déterminés (voir Helfman et Winkleman 1997; Chivers *et al.* 2001; Brown *et al.* 2006).

De plus, les réponses anti-prédateurs telles que la vie en banc et l'utilisation des habitats structurés en tant que refuge ont reçu beaucoup d'attention de la part des chercheurs, mais généralement de façon indépendante et chez des espèces différentes. Par conséquent, les facteurs déterminant l'utilisation d'une tactique ou l'autre dans un contexte donné ont été peu étudiés (Rangeley et Kramer 1998; Krause *et al.* 2000).

Les espèces avec des tactiques anti-prédateurs flexibles, telles le ventre rouge du nord, pourraient donc être particulièrement utiles pour examiner les déterminants écologiques des tactiques anti-prédateurs. De plus, comme le suggère nos résultats, cette flexibilité peut avoir des implications importantes sur les patrons de distribution des individus.

Mécanismes expliquant les migrations journalières

Les migrations journalières horizontales observées chez les ventres rouges du nord persistent dans des lacs où les prédateurs pélagiques sont absents (Gaudreau et Boisclair 1998), ce qui suggère que d'autres hypothèses pourraient expliquer ce comportement. La première serait que ces migrations seraient déterminées génétiquement et persisteraient même en absence des pressions de sélection responsables du développement de ce comportement (Gliwicz et Jachner 1992; Mehner *et al.* 2007). La deuxième, suggéré par Gaudreau et Boisclair (1998), serait que la profitabilité de l'habitat basculerait de la zone littorale le jour vers la zone pélagique la nuit due à la forte abondance de zooplancton dans la zone pélagique supérieure durant la nuit. Ceci suppose que le mécanisme responsable de ces migrations est la maximisation du taux d'alimentation (et par conséquent du taux de croissance) et non l'évitement des prédateurs. Cette hypothèse ne peut pas expliquer les migrations journalières observées dans les lacs de notre étude. En effet, les biomasses de zooplancton dans la zone pélagique étaient équivalentes le jour et la nuit (Annexe A). La troisième serait que les migrations de la zone pélagique vers la zone littorale pourraient être causées par la température de l'eau, puisque se déplacer d'une zone plus froide vers une zone plus chaude accélèrerait le métabolisme et la croissance, pourvu que la nourriture soit suffisamment abondante (Neverman et Wurstsbaugh 1994; Garner *et al.* 1998). Ces trois hypothèses, i.e., l'évitement des prédateurs, la maximisation du taux d'alimentation et l'efficacité bioénergétique, ne sont pas mutuellement exclusives et peuvent expliquer les migrations journalières (verticales et horizontales) observées chez beaucoup d'espèces de poissons (Helfman

1993). L'importance relative de chaque mécanisme et leurs effets sur l'amplitude spatiale et temporelle des migrations restent à être déterminés.

Conséquences écologiques du risque de prédation

Notre étude, comme beaucoup d'autres (Lima et Dill 1990; Lima 1998), a démontré que les décisions comportementales prises par les individus face au risque de prédation pouvaient fortement influencer leur utilisation des habitats. A long terme, les décisions qui permettent de réduire le risque de prédation mènent également à une diminution des opportunités de s'alimenter, ce qui entraîne une diminution du taux de croissance ou de la condition corporelle des individus, et finalement, du taux de reproduction (Lima 1998). On peut donc s'attendre à ce que ces décisions influencent différents aspects de la dynamique et de la régulation des populations de proies. Cependant, on connait peu de choses sur les conséquences de ces décisions comportementales à l'échelle des populations dû au fait que les études couvrant une population entière de proies sont rares (mais voir Werner *et al.* 1983; Tonn *et al.* 1992; Diehl et Eklov 1995). Le système prédateur-proie utilisé dans notre étude serait un bon modèle biologique pour étudier cette question. En effet, l'utilisation accrue de la zone littorale par les ventres rouges du nord dans les lacs où le risque de prédation est plus élevé (et donc l'évitement de la zone principale d'alimentation, la zone pélagique; Chapitre III) pourrait influencer les taux de croissance et de reproduction des individus dans ces lacs (comparé à des lacs où le risque de prédation est plus faible). Ainsi, on pourrait s'attendre à ce que la dynamique des populations de ventres rouges du nord varie d'un lac à l'autre en fonction de l'intensité du risque de prédation.

Ce système serait également un bon modèle pour comprendre les conséquences des effets indirects des prédateurs sur la dynamique et la structure des communautés. Les prédateurs ont des effets directs sur leur proie, en diminuant leur abondance ou en altérant leur comportement (p. ex., leur comportement alimentaire ou leur utilisation des habitats). Mais les prédateurs ont également des effets indirects

sur les communautés, dû au fait que les changements de comportement induits chez leur proie peuvent avoir des répercussions sur la ressource de cette proie, ou sur tout autre espèce qui interagit avec cette proie (Abrams 1995). Bien que l'on soit conscient de l'existence de ces effets indirects, on connait peu de choses sur leur importance dans la structure et la dynamique des communautés (Luttbeg et Kerby 2005). De plus, il serait important de prendre en considération ces interactions indirectes dans un contexte de conservation et de gestion des écosystèmes (Carpenter et Kitchell 1993; Dill 2003). Les effets de ces interactions indirectes sur les chaînes trophiques et les interactions interspécifiques peuvent être importants quand les prédateurs influencent l'utilisation de l'habitat par leur proie (Werner 1992; Diehl et Eklov 1995; Persson *et al.* 1996; Lima 1998). Ainsi, le système prédateur-proie utilisé dans notre étude serait encore une fois un bon modèle biologique pour étudier cette question. En raison de l'utilisation accrue de la zone littorale par les ventres rouges du nord en réponse à l'augmentation du risque de prédation, on pourrait s'attendre à ce que (i) la pression de prédation sur le zooplancton par les ventres rouges du nord et (ii) l'intensité des interactions interspécifiques entre les espèces partageant la zone littorale avec les ventres rouges du nord (i.e., le meunier noir et le mulet à cornes) et ce dernier varient d'un lac à l'autre, en fonction de l'intensité du risque de prédation. Donc, d'une manière générale, l'importance et les conséquences des effets indirects de la prédation sur la dynamique et la structure des communautés devraient être différentes d'un lac à l'autre.

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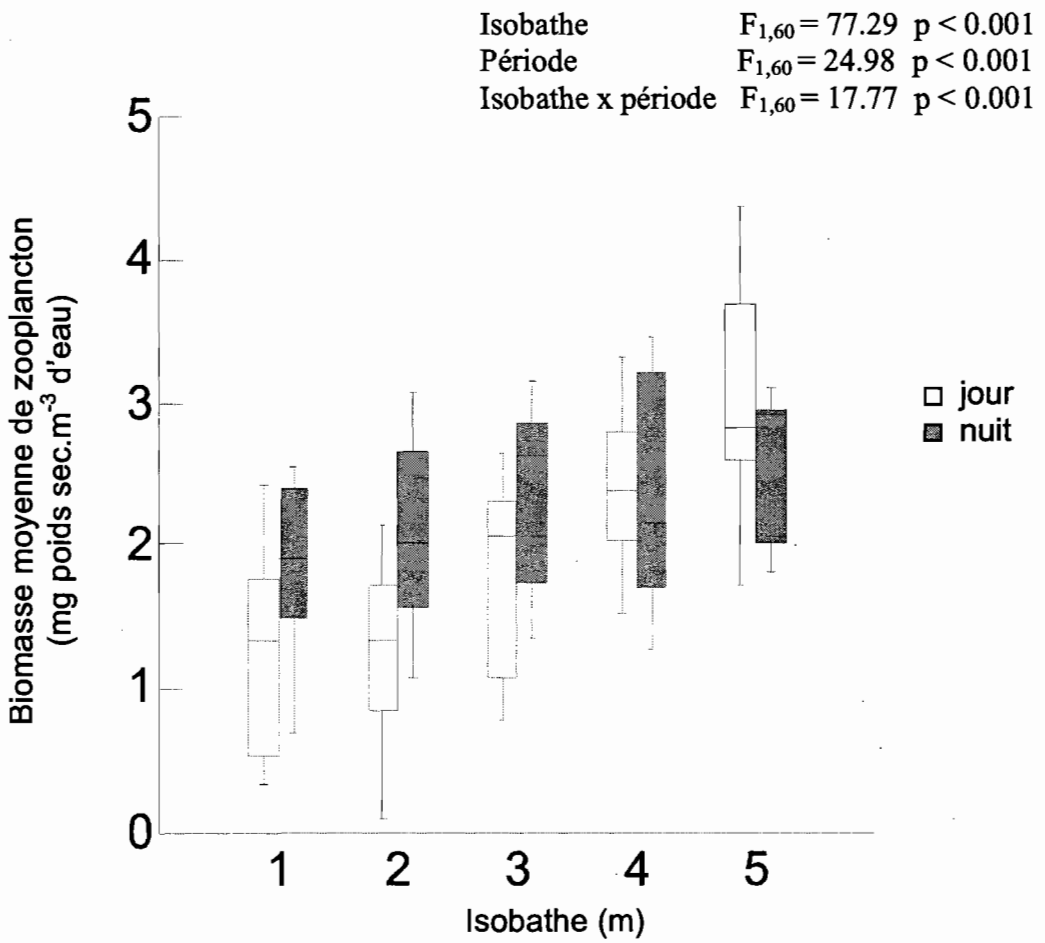
ANNEXE A

Box plot représentant la variation de la biomasse moyenne de zooplancton (taille > 500 μm ; transformé en Log(X + 1)) situé dans la couche supérieure de la colonne d'eau (profondeur < 2 m) en fonction de l'isobathe et de la période de la journée.

Les données proviennent de sept lacs échantillonnés durant l'été 2003 (cf. Chapitre II, Table 1 pour les détails concernant les lacs). Le zooplancton a été échantillonné à l'aide d'un filet Wisconsin (maille 63 μm). Des traits horizontaux de 15 mètres de long parallèles à la berge ont été effectués à différentes isobathes (1, 2, 3, 4 et 5 m), à 0.5 m et à 1.5 m de la surface, à midi et à minuit. Les échantillons ont été préservés dans l'alcool à 95%, et le zooplancton > 500 μm (composé principallement de *Daphnia* et *Holopedium*) a été filtré (filtre en fibre de verre GF/A, Whatman), séché à 40°C pendant 18h, puis pesé.

Un modèle mixte à mesures répétées (PROC MIXED, SAS 9.1.3) a été utilisé afin de déterminer si l'isobathe et la période de la journée influençaient la biomasse moyenne de zooplancton situé dans la couche supérieure de la colonne d'eau.


Isobathe $F_{1,60} = 77.29$ $p < 0.001$
Période $F_{1,60} = 24.98$ $p < 0.001$
Isobathe x période $F_{1,60} = 17.77$ $p < 0.001$
Biomasse moyenne de zooplancton (mg poids sec.m^{-3} d'eau)
0
1
2
3
4
5
1
2
3
4
5
Isobathe (m)
jour
nuit